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ERRATA.

Page 13, line 20, for "*Anagrus*" read "*Anagyrus*"

,, 165, line 14 and p. 166 last line, for "R. N. Krishna Ayyar" read "P. N. Krishna Ayyar"

,, 237, line 2, p. 241 17 lines from end and p. 246 line 5, for "1936" read "1937"

,, 238, 8 lines from end and p. 245 4 lines from end, for "1935" read "1936"

,, 370, line 5, and p. 372, line 16, for "*juxtomansonia*" read "*juxtamansonia*"

,, 372, delete line 20 beginning "*Haemagogus capricorni* . . ."

,, 419, line 5, delete "21"

,, 419, line 7, for "36" read "35"

,, 419, line 8, for "*Anopheles*" read "*Anopheles*†"

,, 419, line 15, insert "62" between "61 and 66"

,, 419, line 17, delete "195"

,, 507, line 30, for "H. St. J. R. Donisthorpe" read "H. St. J. K. Donisthorpe"

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IMPERIAL INSTITUTE OF ENTOMOLOGY.

BULLETIN

OF

ENTOMOLOGICAL RESEARCH.

VOL. 30. 1939.

A SECOND REPORT ON SOME MISCELLANEOUS AFRICAN ENCYRTIDAE IN THE BRITISH MUSEUM.*

By HAROLD COMPERE,

Assistant Entomologist, University of California Citrus Experiment Station, Riverside, California.

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* Paper No. 392, University of California Citrus Experiment Station and Graduate School of Tropical Agriculture, Riverside, California.

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The holotypes and allotypes of all species described as new in this paper are to be deposited in the British Museum and paratypes in the United States National Museum. All the species described in this paper are parasitic in scale-insects or mealybugs.

Some of the classifications presented in these papers on African ENCYRTIDAE are tentative only, for in the case of closely related variable species it is impossible to make final identifications on the basis of a few museum samples. The exact degrees of relationship can be expressed only when the insects are known intimately throughout their entire range and a knowledge of the limits and degrees of variation obtained. Even with this knowledge it is not always possible to make final determinations with assurance.

Genus **Anagyrus**, Howard.

Twelve species of *Anagyrus* from Africa are considered in this paper, seven of which are described as new. Of those previously described, two, namely, *Anagyrus subproximus*, Silvestri, and *A. aurantifrons*, Compere, are known from Africa only. *Anagyrus greeni*, Howard, which was described from specimens collected in Ceylon, is recorded by Mercet as occurring in Egypt. *Anagyrus saccharicola* was described by Timberlake from specimens collected in Natal, Federated Malay States and the Philippine Islands. *Anagyrus swezeyi*, Timberlake, described from specimens collected in Hawaii, is recorded in this paper from Cape Province. The remaining seven species, described as new, are known from Africa only.

Except for *Anagyrus saccharicola* and *A. swezeyi*, which differ greatly and belong to another section of the genus, the species considered here are fundamentally similar and are often difficult to identify. *Anagyrus greeni*, the genotype, may be an exception. It is the only species not available for study. It is known to the writer by the original description only. Howard described the joints of the funicle as subequal, each about one and one-half times as long as the pedicel. In the proportions of the funicle joints relative to the pedicel *greeni* differs from the seven new species as well as from *A. subproximus* and *A. aurantifrons*. In none of these species do the funicle joints exceed the pedicel in length.

The following description includes characters common to all the species of *Anagyrus* mentioned in this paper except *A. saccharicola*, Timberlake, *A. swezeyi*, Timberlake, and possibly *A. greeni*, Howard. Characters given in the general description are not repeated in the descriptions of the individual species.

Characters Common to Anagyrus *of the* subproximus *Group of Species.*

♀♀. Head dorsal view, ranging near twice as wide as long; anterior margin gently concave between the orbits; occipital margin between the orbits more strongly concave than anterior margin; inner orbits gently diverging anteriorly from a point on an imaginary line transverse to the posterior ocelli; frontovertex ranging from as long as wide to almost one and one-half times as long as wide, occupying about one-third the width of head. Head frontal view about one and one-fifth times as wide as high; eyes hairy, large and protuberant below, somewhat more than one and one-half times as long as wide, descending three-fourths the depth of head; cheeks short, strongly convergent below, much shorter than the transverse diameter of the eyes; genal suture distinct; antennae much closer to the oral margin than to the orbits, sockets with the upper margins about tangential to the basal ocular line; scrobes slightly convergent above, almost perpendicular, not polished, nor joined above, separated by a gently, convexly rounded ridge plainly visible in profile but not in dorsal view if the head is exactly vertical. Integument of frontovertex, face, cheeks, and temples non-metallic, opaque, very minutely alutaceous; clothed with slightly flattened, silvery hairs.

Antennal scape flattened and expanded below, measuring near twice as long as wide, largely black; near the apex encircled by an oblique, irregular white band; near the base encircled or with a rounded or rectangular white mark on outer aspect; pedicel cylindrical in cross section, two to three times as long as wide, completely black or with the apical portion more or less white. First funicle joint usually completely black, ranging from one and one-half to three times as long as wide; funicle joints generally increasing slightly in width and decreasing slightly in length distad so that the sixth is plainly shorter and wider than the first; distal five funicle joints and club often white with fine white hairs, transparent in balsam; club slightly wider than the sixth funicle joint and usually plainly shorter than the three preceding joints together.

Notum of thorax slightly convex, the scutellum less so than the mesoscutum. Pronotum short, the collar usually more or less testaceous or silvery in contrast to the mesoscutum. Mesoscutum almost twice as wide as long, usually covered with numerous silvery, slightly flattened hairs ; the integument minutely and intricately sculptured. Axillae slightly separated at inner ends, the disks almost flush with the plane of the mesoscutum and scutellum. Scutellum large, acutely triangular, as long as wide and slightly longer than the mesoscutum, slightly elevated, with narrow vertical sides. Tegulae white basally and more or less blackish distally. Metanotum and propodeum black or mostly so, intricately sculptured, the latter with silvery hairs on sides. Sides of thorax testaceous or largely so ; prepectus transparent white posteriorly and testaceous anteriorly.

Abdomen after shrinkage, elongate triangular, narrowly acute at apex, about as long as the thorax ; cercal plates near the base. Ovipositor shortly exserted. When it is thrust out, the ovipositor extends horizontally and the ventrites are extruded. Abdomen black or largely so, the sides and dorsum covered with white or silvery hairs and the integument intricately sculptured.

Forewings more than twice as long as wide, in repose extending well beyond the apex of the abdomen. Submarginal vein of about uniform width throughout, with a row of coarse, erect stiff hairs, terminating distally at a hyaline break which defines the junction of the submarginal and marginal veins. The speculum separated anteriorly from the marginal and stigmal veins by two or three rows of fine, short, hairs ; near the middle of the blade, or posterior to the middle, the speculum interrupted by from three to eleven uneven irregular rows of fine hairs such as cover the disk, the posterior basal portion often rounded and separated by two or three rows of hairs from the posterior margin of blade.

Legs slender ; spur of middle tibiae slightly shorter than the basitarsus, the latter about as long as the four succeeding joints together. Generally the legs are sordid white with faint admixtures of testaceous and in parts suffused with fuscous. The fuscous suffusions are often indistinct and irregular. Unless the leg markings are distinct and sufficiently different to justify describing no mention is made of them in the descriptions of the individual species.

Integument of head and thorax sufficiently thick and rigid so that after drying specimens usually retain their shape.

The species of *Anagyrus* are numerous and many of them are difficult to recognize because of their close resemblance to each other. The characters used to separate some species are minute and elusive. Until more precise methods of examination and description are used it will be very difficult for one without specimens for reference to interpret what is intended by a sentence such as : " Eyes thickly and coarsely hairy." The coarseness and the density of the hairs which clothe the eyes differ among the species. At one extreme under ordinary powers of magnification the eyes appear glabrous, the very small hairs not evident. At the other extreme, at the same magnification, in species such as *A. aurantifrons*, the eyes appear thickly and coarsely hairy. Between these extremes are intergradations. The dimensions of the heads differ within narrow limits. Unless the heads are oriented so as to be in exactly the same positions and are measured precisely across the same points a term such as " frontovertex slightly longer than wide (5 : 4) " cannot be depended upon. The measurements of the head given in this paper were obtained with the heads in an exact vertical position ; the length of the frontovertex measured along the median line from the anterior to the posterior concave margins ; the width measured across the narrow portion about in line with the posterior ocelli. A slight tilting of the head from the vertical position results in a different set of measurements from those obtained with the head exactly vertical. The differences in the venation, especially in the length of the postmarginal vein relative to the length of the marginal vein, are of value. In interpreting the drawings of the venation, allowance should be made for variation within the species ; no two specimens appear exactly identical.

Key to the African Species of Anagyrus, *Females.*

1. Frontovertex plainly narrower than the length of scape or transverse diameter of the eyes. Abdomen shorter than the head and thorax united............3

Frontovertex about as wide as or wider than the length of scape or transverse diameter of the eyes. Abdomen longer than the head and thorax united...2

2. Second and third funicle joints whitish, the others blackish. Frontovertex about as wide as the transverse diameter of the eyes. Antennae inserted above the oral margin by a distance equal to approximately the length of an antennal socket. Scrobes perpendicular, ascending fully twice as far as the length of an antennal socket and ending far above the basal level of the eyes. Notum of thorax not depressed after drying (Cape Province)... 1. *swezeyi*, Timberlake

First funicle joint black, the other funicle joints and club white. Frontovertex wider than the transverse diameter of the eyes. Antennae inserted above the oral margin by a distance equal to approximately one-half the length of an antennal socket. Scrobes convergent but not joined above; ascending scarcely as far as the length of an antennal socket and ending shortly above the basal level of the eyes. Head and thorax ferruginous. Notum of thorax depressed after drying (Natal)........................2. *saccharicola*, Timberlake

3. First funicle joint not longer than the pedicel..4

First funicle joint one and one-half times as long as the pedicel, all funicle joints subequal. Ocelli in a right-angled triangle. General colour dull reddish yellow; scape and pedicel black, whitish at tips; first funicle joint black, the others and club white (Egypt).....................3. *greeni*, Howard

4. Notum of thorax dominantly ferruginous..9

Notum of thorax black, or with slight admixtures of ferruginous on sides of mesoscutum..5

5. Distal four or five funicle joints and the club white..................................7

Distal five funicle joints black or diluted with black.................................6

6. Apex of pedicel white; first funicle joint black, the succeeding funicle joints and club diluted with black. First funicle joint three times as long as wide (Eritrea)..4. *abyssinicus*, sp. n.

Apex of pedicel black concolorous with base, the succeeding funicle joints blackish; club mostly white, the base diluted with blackish. First funicle joint two and one-half times as long as wide (Uganda).......................... 5. *bugandaensis*, sp. n.

7. Frontovertex ferruginous or mostly so...8

Frontovertex black except narrowly along the orbits. Ocelli in a right-angled triangle. Speculum interrupted by eight rows of hairs, the basal cut-off portion twice its own diameter from the anterior portion (Transvaal)......... 6. *nigrescens*, sp. n.

8. Speculum interrupted by three or four rows of hairs, the basal cut-off portion less than its own diameter from the anterior portion (Uganda)................. 7. *niger*, sp. n.

Speculum interrupted below by nine rows of hairs, the basal cut-off portion fully twice its own diameter from the anterior portion (Eritrea)................ 8. *pullus*, sp. n.

9. First funicle joint plainly more than one and one-half times as long as wide...11

First funicle joint one and one-half times as long as wide and plainly shorter than the pedicel..10

10. Ocelli in a right-angled triangle or nearly so. All of cheeks and most of face below and between antennal sockets, black. Scape narrowly white at base and with a distinct, prebasal rounded white spot. Cheeks, notum of thorax, sides of propodeum, and the abdomen with the short, flattened silvery hairs coarser and thicker than in the following species. Notum of thorax more extensively diluted with black than in the following species; the anterior portion and sides of mesoscutum, most of axillae, centre, and sides of scutellum plainly blackish. Speculum interrupted by nine rows of hairs, the small rounded basal portion fully twice its own diameter from the anterior portion. Scutellum with three pairs of coarse black setae toward the apex (Belgian Congo)..9. *kivuensis*, sp. n.

Ocelli in plainly less than a right-angled triangle. Cheeks mesad of the genal suture and face below and between the antennal sockets testaceous or mostly so. Scape indistinctly narrowly margined with white at base and without a prebasal rounded white spot. Cheeks, notum of thorax, sides of propodeum and the abdomen with the short flattened silvery setae not so conspicuous as in the preceding species. Notum of thorax almost completely testaceous or with slight intrusions of blackish. Speculum interrupted by six rows of hairs, the basal hairless spot less than twice its own diameter from the anterior portion. Scutellum with two pairs of coarse, black setae toward the apex (Transvaal)..10. *amoenus*, sp. n.

11. First funicle joint plainly less than three times as long as wide and not much longer than the sixth funicle joint. Funicle joints distad of the first, faintly flushed with dusky on ventral aspects and the dark areas provided with dusky hairs. Postmarginal vein subequal in length to the marginal vein (Eritrea)..11. *subproximus* (Silvestri)

First funicle joint usually three times as long as wide and plainly longer than the sixth funicle joint. Funicle joints distad of the first, pale white. Postmarginal vein plainly shorter than the marginal vein (Cape Province)......... 12. *aurantifrons*, Compere

Key to the African Species of Anagyrus, *Males.**

1. Scape white basally or largely so..2

Scape black except ventrally near the apex which is white; twice as long as wide. Flagellum blackish, the basal portion more intensively so. Face and cheeks black. Mesopleura brown (Uganda).................*bugandaensis*, sp. n.

2. Forewings without an extensive area on the blade below the venation, furnished with fine white hairs that are transparent in balsam............................3

Forewings with the greater part of the blade below the venation, furnished with white hairs that are transparent in balsam. Marginal and postmarginal veins somewhat thicker than in the other species. Face and cheeks black. Frontovertex twice as wide as long and occupying more than one-half the width of head (Transvaal)..*nigrescens*, sp. n.

3. Marginal vein longer than wide; the marginal and post-marginal veins together about as long as the stigmal vein...4

Marginal vein wider than long; the marginal and post-marginal veins together about one-half as long as the stigmal vein. Scape almost three times as long as wide, white narrowly beneath at apex and on basal half; pedicel and apex of the club blackish, remainder of flagellum whitish (Belgian Congo)........... *kivuensis*, sp. n.

---

* Six of the African species are represented by males. In the male sex the species are even more difficult to separate than in the female sex

4. First funicle joint from three to slightly less than four times as long as wide...5

First funicle joint four times as long as wide, as long as the scape (Cape Province) *aurantifrons*, Compere

5. Scape white on basal half and for entire length on ventral margin. Scutellum with two pairs of long, coarse hairs on distal half (Transvaal)...*amoenus*, sp. n.

Scape white on basal half and near apex beneath, the intermediate portion blackish. Scutellum with three pairs of long, coarse hairs on distal half (Eritrea)...*subproximus* (Silvestri)

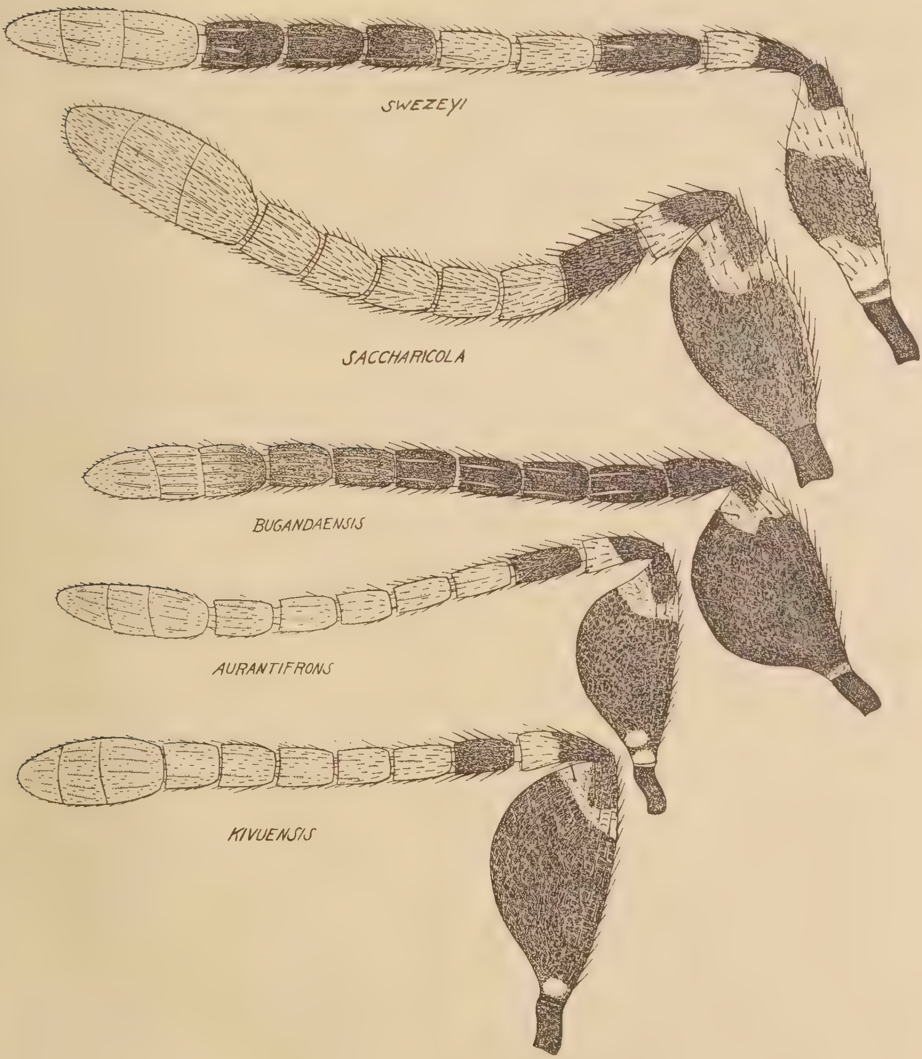
SWEZEYI
SACCHARICOLA
BUGANDAENSIS
AURANTIFRONS
KIVUENSIS

Fig. 1. *Anagyrus* spp., ♀♀; antennae.

1. **Anagyrus swezeyi,** Timberlake (fig. 1).

Anagyrus swezeyi, Timberlake, Proc. Haw. Ent. Soc. **4** (1), 1919, pp. 199–201.

1 ♀ mounted on slide, labelled " Taken on window, Rosebank, Cape Province, So. Africa, 25.iii.1925, E. W. Rust."

2. **Anagyrus saccharicola,** Timberlake (fig. 1).

Anagyrus saccharicola, Timberlake, Proc. Haw. Ent. Soc., **8** (1), 1932, pp. 159–162.

This species was reared by Rust, from an unidentified mealybug collected at the Tsetse-fly Laboratory, Zululand, Natal, 10.xii.1925.

3. **Anagyrus greeni,** Howard.

Anagyrus greeni, Howard, Proc. U.S. Nat. Mus., **18** 1896, p. **369,** Mercet, Bull. Soc. Roy. Ent. Egypte, **9,** 1925, p. 46.

This species was recorded from Africa by R. G. Mercet. The characters used in the key were obtained from Howard's original description.

4. **Anagyrus abyssinicus,** sp. n. (figs. 2, 3).

♀. Frontovertex and part of face orange-yellow ; cheeks blackish laterad of genal suture ; the elevated area between scrobes and above the oral margin black. Notum of thorax mostly black, with flattened, silvery hairs ; collar of pronotum testaceous to silvery ; abdomen black ; sides of pronotum and mesopleura orange-yellow. Scape with a more or less quadrate or angular prebasal white spot and the usual preapical oblique white band ; pedicel black basally and white apically ; first funicle joint black ; distal five funicle joints and club fusco-testaceous. Legs with rather pronounced dilutions of blackish or brown most evident on parts of coxae and on dorsal and ventral aspects of femora and tibiae.

Frontovertex as wide as long ; ocelli in a right-angled triangle or nearly so. Eyes plainly hairy. Pedicel about two and one-half times as long as wide ; first funicle joint three times as long as wide, as long as the pedicel and almost one and one-half times as long as the sixth funicle joint ; sixth funicle joint slightly less than twice as long as wide. Postmarginal vein shorter than the marginal vein. Speculum interrupted by seven rows of hairs ; the basal cut-off portion separated by slightly more than its own diameter.

Length 1·5 mm.

Described from 2 ♀♀, holotype and paratype reared from a *Pseudococcus* sp. on *Ficus*, Giglasciu, Eritrea, 27.iv.1930, H. Compere.

5. **Anagyrus bugandaensis,** sp. n. (figs. 1, 3).

Anagyrus quercicola, described from Spain by Mercet, has the funicle entirely blackish as in this species. *A. quercicola* is described as having the ocelli in an equilateral triangle, notum of thorax partly ferruginous and the pedicel white apically. *A. bugandaensis* is also closely related to *A. abyssinicus* from which it is distinguished by the characters given in the key.

♀. Frontovertex yellow to golden brownish, grading to black or brown near the ocelli ; face, cheeks and temples largely blackish. Notum of thorax completely black and on the sides of mesoscutum, axillae and scutellum with faint intrusions of ferruginous ; collar of pronotum concolorous with mesoscutum or slightly paler ; abdomen black ; mesopleura yellowish to sordid white ; sides of propodeum slightly suffused with brownish yellow. Scape narrowly and indistinctly margined with white at base and without a prebasal white mark. Pedicel entirely black. First funicle joint black, the succeeding joints grading from black to dilute blackish ;

basal club joint suffused with blackish basally, the distal joints whitish. Legs with rather distinct blackish dilutions.

Frontovertex slightly wider than long (9 : 8) ; ocelli in a right-angled triangle or nearly so. Pedicel about twice as long as wide and slightly shorter than the first funicle joint (6 : 7) ; first funicle joint about as long as the pedicel, slightly more than twice as long as wide (7 : 3) and almost one and one-half times as long as the sixth funicle joint (7 : 5), sixth funicle joint almost one and one-half times as long as wide (5 : 3). Postmarginal vein slightly shorter than the marginal vein ; marginal vein about as long as wide. Speculum interrupted by five rows of hairs, the basal cut-off portion separated by slightly more than its own diameter. Eyes moderately hairy.

Length 1·5 mm.

♂. Head except mouth-parts, notum of thorax and abdomen black ; mesopleura brown ; legs largely whitish with darker suffusion in parts. Scape twice as long as wide, mostly black, white beneath near the apex ; pedicel and first two or three funicle joints black, the following paler.

Described from 3 ♀♀ and 3 ♂♂, holotypes, allotype, and paratypes, reared from *Pseudococcus kenyae*, Le Pelley, Kampala, Uganda, xi.1935 by F. B. Notley. This series of specimens bears Ferrière's No. 17 and Notley's Nos. 513 to 519.

6. **Anagyrus nigrescens,** sp. n. (figs. 2, 3).

♂. Frontovertex, face, cheeks and temples black except along the orbits which may be narrowly marked with ferruginous on the frontovertex. Notum of thorax black ; collar of pronotum concolorous with mesoscutum or nearly so ; abdomen black ; sides of pronotum and the mesopleura testaceous or mostly so. Scape with an indistinct prebasal white mark on outer aspect ; pedicel black basally and white distally ; first funicle joint mostly black, white at distal end ; distal five funicle joints and club white. Notum of thorax, sides of propodeum, and the abdomen with flattened silvery hairs which are coarse and conspicuous in contrast to those of some species. Fore and hind legs with distinct black suffusions, the middle legs yellowish white without blackish suffusion.

Frontovertex plainly wider than long (3 : 2) ; ocelli in a right-angled triangle. Pedicel twice as long as wide ; first funicle joint twice as long as wide, as long as the pedicel and plainly longer than the sixth funicle joint ; sixth funicle joint slightly longer than wide. Marginal, postmarginal, and stigmal veins rather coarse ; postmarginal vein shorter than the marginal vein, the two united as long as the stigmal vein. Forewings toward the base and posteriorly with fine, white hairs that become transparent in balsam-mounted specimens. Speculum interrupted by eight rows of white hairs, the basal cut-off portion separated by twice its own diameter. Eyes with moderately sparse but long hairs.

Length 1·3 mm.

♂. Head and body black except the basal part of tegulae and the prepectus, the former white and the latter testaceous ; all coxae black ; posterior femora blackish except near distal end ; flagellum grading from black basally to fusco-testaceous apically.

Described from 29 ♀♀ and 20 ♂♂, holotype, allotype and paratypes as follows : 10 ♀♀ and 9 ♂♂ reared at Riverside, California, from a *Pseudococcus* sp. collected at Johannesburg, Transvaal, iv.1937, by H. Compere ; 19 ♀♀ and 11♂♂ reared from a *Pseudococcus* alleged to be *citri*, Pretoria, Transvaal, 1.ix.1919, by E. W. Rust. The mealy-bug parasitized by *A. nigrescens* in Johnnesburg was taken either on shade trees or on oleander.

7. Anagyrus niger, sp. n. (fig. 3).

♀. Frontovertex and portions of the face and cheeks golden yellow ; cheeks beneath the orbits, elevation between scrobes and area enclosed by the ocelli blackish. Notum of thorax and abdomen black ; sides and sternum of thorax except propodeum testaceous. Scape with a white spot on outer aspect near base ; pedicel black on basal two-thirds, white apically ; first funicle joint entirely black ; second funicle joint white diluted with fuscous ; remainder of antennae white. Legs whitish or pale yellowish with fuscous suffusions as follows : dorsal aspect of front coxae ; dorsal

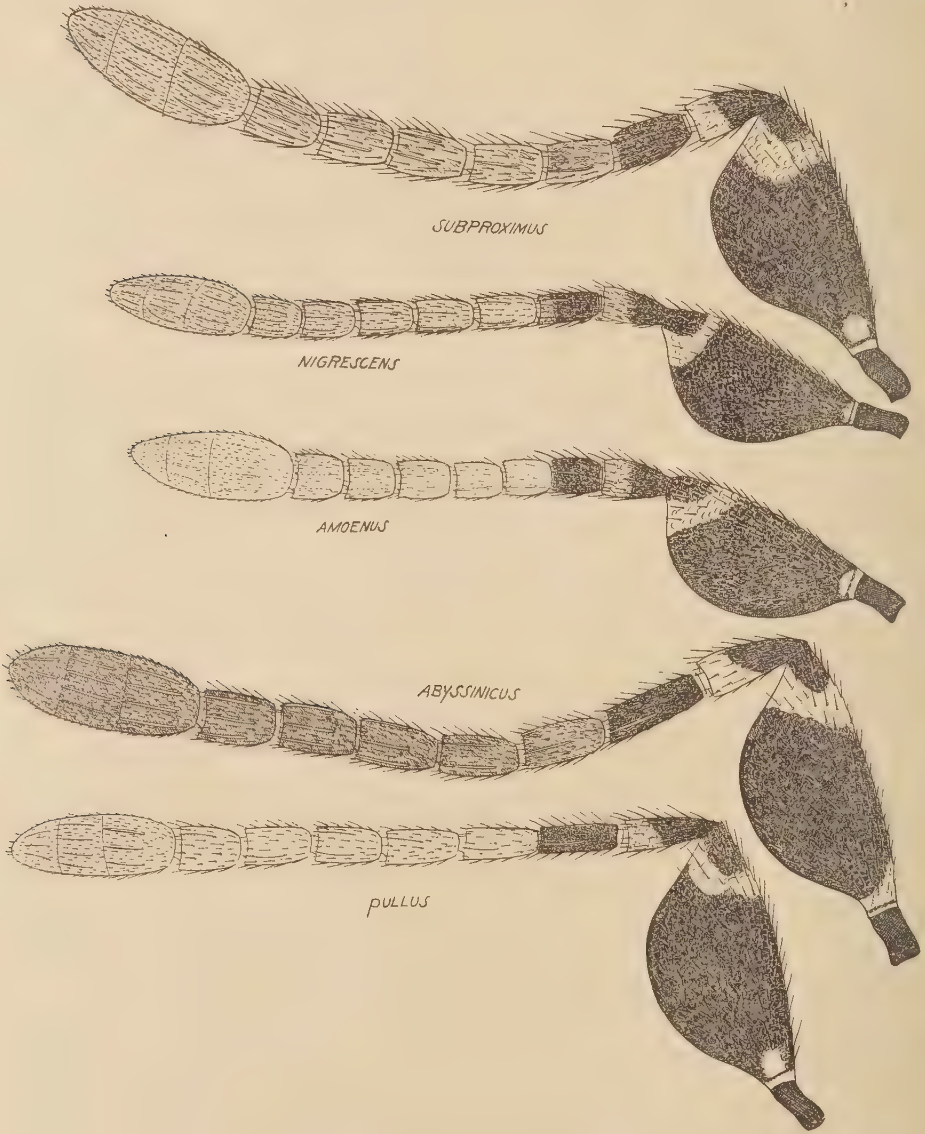

Fig. 2. *Anagyrus* spp., ♀♀ ; antennae.

and ventral aspects of front femora ; dorsal aspect of middle femora ; dorsal aspect of middle tibiae toward base ; exposed aspects of middle and hind coxae ; dorsal aspect of hind tibiae conspicuously blackish. Eyes pale gray. Dorsum of head without silvery flattened hairs. Notum of thorax with hairs slightly less flattened and less silvery than in other blackish species. Eyes with short, coarse hairs.

Frontovertex as long as wide. Ocelli in an isosceles triangle, the posterior ocelli less than once their own diameter from orbits and slightly farther from the occipital margin. Scape slightly more than twice as long as wide (13 : 6) ; pedicel three times as long as wide ; first funicle joint equal in length to the pedicel and about three times as long as wide ; sixth funicle joint about two-thirds as long as the first and slightly less than twice as long as wide (13 : 7). Stigmal vein longer than the marginal and postmarginal together (8 : 5) ; marginal vein less than twice as long as wide ; postmarginal vein very short. Speculum interrupted by four rows of hairs, the basal cut-off part separated by its own length.

Length 2·1 mm.

Described from 1 ♀, holotype, reared from a *Pseudococcus* sp. on oleander, Masaka, Uganda, vii.1937, by H. Compere.

8. **Anagyrus pullus,** sp. n. (figs. 2, 3).

♀. Frontovertex and the face above the antennal sockets exclusive of cheeks and the prominence between scrobes orange-yellow ; cheeks and interscrobal prominence black. Notum of thorax dominantly black ; sides of mesoscutum with slight suffusions of ferruginous ; collar of pronotum faintly silvery testaceous ; mesopleura and sides of pronotum testaceous. Scape with a distinct, rounded white spot on outer aspect near base ; basal two-thirds of pedicel black, the apex white ; first funicle joint black ; remainder of flagellum white. Legs whitish with suffusions of blackish.

Eyes very minutely hairy, appearing bare under ordinary magnifications. Hairs on notum of thorax less squamous and silvery than in *A. nigrescens* and more squamous and silvery than in *A. niger*. Frontovertex slightly longer than wide (11 : 10). Ocelli in an equilateral triangle, the posterior pair slightly less than their own diameter from the orbits and about the same distance from the occipital margin. Marginal vein less than twice as long as wide, about twice as long as the postmarginal, the two together not quite so long as the stigmal vein. Speculum interrupted by nine rows of hairs, the basal cut-off portion separated by fully twice its own diameter.

Length 1·7 mm.

Described from 7 ♀♀, holotype and paratypes, reared from a *Pseudococcus* sp. on *Olea chrysophylla*, Nefasit, Eritrea, iii, iv.1930, by H. Compere.

9. **Anagyrus kivuensis,** sp. n. (figs. 1, 3).

♀. Frontovertex orange-yellow ; lower portion of face and the cheeks extensively blackish. Notum of thorax variable, the blackish suffusions are dominant in some specimens, but in general ferruginous appearing to be the basic colour suffused in parts by blackish ; collar of pronotum silvery testaceous ; sides of pronotum and mesopleura testaceous, sometimes with intrusions of blackish or brown. Scape with a distinct rounded white spot on outer aspect near base ; basal half of pedicel black, white at apex ; first funicle joint black, remainder of flagellum white. Legs whitish to pale testaceous with slight suffusions of dusky or blackish.

Eyes minutely hairy. Hairs on cheeks, lower face, notum of thorax, sides of propodeum, and abdomen somewhat more conspicuous than usual. Frontovertex slightly longer than wide (12 : 11). Ocelli in a right-angled triangle ; the posterior pair about their own diameter from the orbital and occipital margins. An outstanding diagnostic character is the relatively short first funicle joint as compared with the length of pedicel. Pedicel a trifle more than twice as long (11 : 5) ; first funicle joint plainly shorter than the pedicel (7 : 11), twice as long as wide and subequal in length to the sixth funicle joint. Marginal and post-marginal veins very short, the two together much shorter than the stigmal vein ; speculum interrupted below by nine or so rows of hairs ; the basal, cut-off portion small, separated by almost thrice its own diameter.

Length 1·2 mm.

♂. Head and thorax black. Hind coxae black ; middle coxae mostly black ; fore coxae slightly suffused with blackish on exposed aspect near base.

Described from 6 ♀♀ and 1 ♂, holotype, allotype, and paratypes, reared from *Pseudococcus* sp., Belgian Congo, 7.v.1937, by A. R. Melville. These specimens bear Ferrière's No. 18 and Melville's No. C-188.

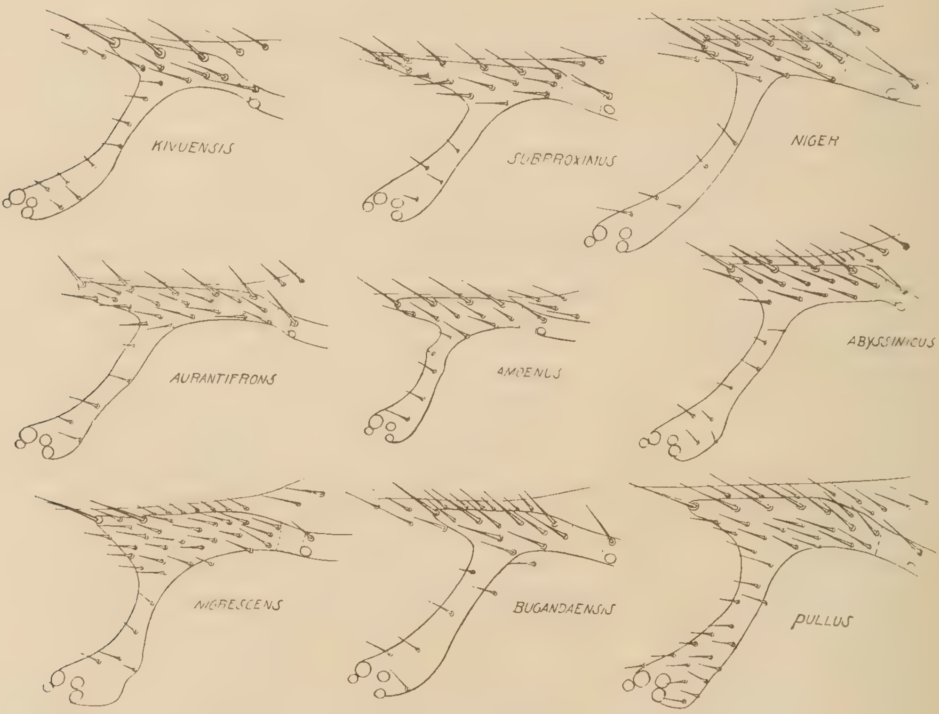

Fig. 3. *Anagyrus* spp., ♀♀ ; venation.

10. Anagyrus amoenus, sp. n. (figs. 2, 3).

This species is very closely related to *A. kivuensis*. All the characters for the identification of this species have been given in the key to the species and in the general description.

♀. Length 1·1 mm.

♂. Frontovertex, face and cheeks with intrusions of ferruginous, the blackish strongly predominant. Sides of thorax largely ferruginous. Frontovertex almost twice as wide as long. Ocelli in an obtuse triangle, the posterior pair more than their own diameter from the orbits and less than one-half their own diameter from the occipital margin.

Described from 8 ♀♀ and 3 ♂♂, holotype, allotype and paratypes, reared in the quarantine room in the insectary of the Citrus Experiment Station at Riverside, California, from a *Pseudococcus* collected either on oleander or shade trees at Johannesburg, Transvaal, iv.1937, by H. Compere.

11. **Anagyrus subproximus** (Silvestri) (figs. 2, 3).

Blastothrix subproxima, Silvestri, Boll. Lab. Zool. Gen. Agr., Portici, **9,** 1914, pp. 346–48.

A series of specimens reared from a *Pseudococcus* sp. on *Olea chrysophylla* at Nefasit, Eritrea, iii, iv.1930, by H. Compere, are identified as *Anagyrus subproximus* (Silvestri). In the original description Silvestri stated that the post-marginal vein is slightly longer than the marginal vein ; pedicel as long as the first funicle joint. The comparatively long post-marginal vein is an important character for the identification of this species. Funicle joints beyond the first slightly flushed with dusky.

12. **Anagrus aurantifrons,** Compere (figs. 1, 3).

Anagyrus aurantifrons, Compere, Univ. Calif. Publ. Entom., **4** (1), 1926, pp. 15–18.

This species is very similar to *A. pseudococci*, Girault, described from specimens collected in Sicily. In *A. pseudococci* the eyes are more coarsely and densely hairy, the head thinner fronto-occipitally, measuring slightly more than twice as wide as long (24 : 11) ; frontovertex as wide as long ; marginal vein plainly less than twice as long as wide. In. *A. aurantifrons* the head is twice as wide as long ; frontovertex slightly longer than wide (5 : 4) ; marginal vein about twice as long as wide. In the original description of *A. aurantifrons* it was stated that the ocelli are in an obtuse triangle. This was a mistake, the ocelli are in an isosceles triangle.

Anagyrus aurantifrons is a common parasite in Cape Province of the mealybug alleged to be *Pseudococcus citri* (Risso).

Genus **Tropidiophryne,** Compere.

Tropidiophryne, Compere, Univ. Calif. Publ. Entom., **5** (14), 1931, pp. 269–72.

In the species of *Tropidiophryne* the funicle joints seem to be in the process of reduction and the original generic description is amended to provide for a variable number of funicle joints. In the original description it was stated, " five funicle joints . . . ; first and second joints not always distinctly separated since the first is small and fits closely." It would have been more accurate to have stated, funicle with four distinct joints and a fifth segment at base not individually articulated nor separately cut off dorsally. The new species, *natalensis*, has three distinct funicle joints. The basal joint is divided below the point of articulation, the divided ventral expansion producing the appearance of a four-jointed funicle. The new species *melvillei* is similar to *africanus* in having four distinct joints in the funicle with the basal segment partly divided so that five segments appear along the ventral margin although there may be only four articulations.

A mistake was made in referring the Australian species *flandersi*, Compere, to *Tropidiophryne*. This Australian species is not congeneric with the species included here. The three species of *Tropidiophryne* can be separated by the characters given in the following key.

Key to the Species of Tropidiophryne, *Females.*

1. Funicle with four distinct joints, sometimes with vestigial fifth joint at base. Frontovertex with numerous, close setiferous punctations in combination with punctate or semi-punctate reticulations. Eyes with almost imperceptible, microscopic pubescence 2

Funicle with three distinct joints and a vestigial fourth joint at base. Frontovertex almost smooth except for very small and widely spaced setiferous punctations. Eyes with distinct, fine sparse setae that are almost as long as the diameter of an ocellus (Natal) .... 1. *natalensis*, sp. n.

2. Ocelli in an acute triangle. Antennal club as long as wide. Mesoscutum and scutellum rather dull, brownish black with intrusions of testaceous. Head dominantly testaceous (Natal, Eritrea) .... 2. *africana*, Compere

Ocelli in a right angle or nearly so. Antennal club longer than wide. Mesoscutum and scutellum dark bluish, sub-metallic. Head dominantly dark, in parts metallic bluish (Kenya Colony) .... 3. *melvillei*, sp. n.

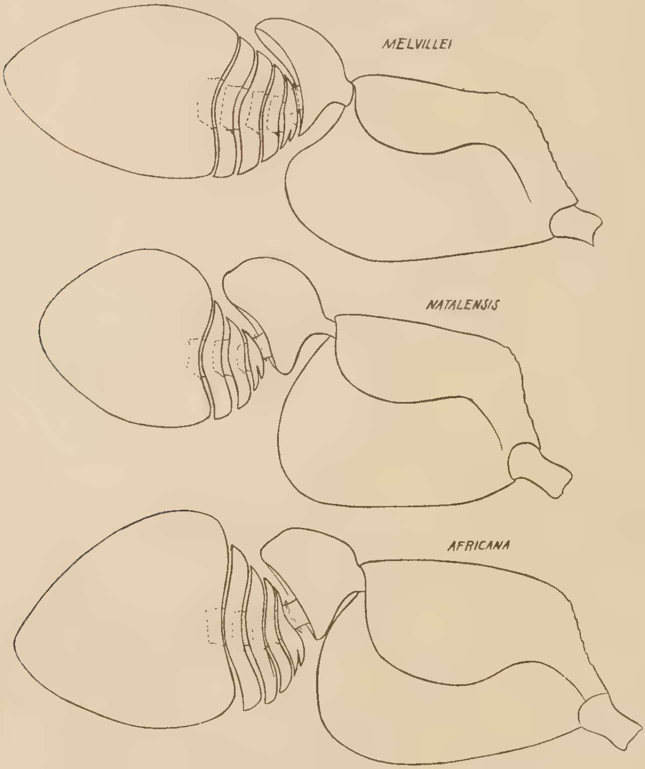

Fig. 4. *Tropidiophryne* spp., ♀♀; antennae.

1. Tropidiophryne natalensis, sp. n. (fig. 4).

Among some unmounted specimens, in the collection of the Citrus Experiment Station, obtained by E. W. Rust in South Africa, are two specimens of *Tropidiophryne* bearing his number Z–15. This was the number given by Rust to the series of specimens mounted by him on slides which form part of the type series on which the description of *T. africana* was based. These two newly acquired specimens represent two distinct species ; one is identified as *T. africana*, and the other is made the holotype of *natalensis*, sp. n. In tag mounts it is almost impossible to see the flagellum, since it is retracted into the fold of the scape. An antenna and wing were detached from the tag mount and mounted directly in balsam. This antenna was unsatisfactory for study, so the head and body with the remaining antenna and wings were boiled in KOH, cleared and mounted. Some notes were made before treating the specimen.

♀. Head, thorax, and abdomen dominantly testaceous ; face below antennae, pleura, and sternum of thorax colourless or whitish ; collar of pronotum, mesoscutum, axillae, and scutellum slightly suffused with brown, sub-metallic. Tibiae and tarsi faintly testaceous, remainder of legs colourless or whitish.

Frontovertex about twice as long as wide (15 : 7) and at narrowest part occupying less than one-third the head width (7 : 23). Ocelli in an acute triangle ; posterior pair about one and one-half times their own diameter apart and almost contiguous with the orbits.

Antennae as shown in fig. 4. Except for the differences mentioned here and in the key and those shown in the figures, the species closely resembles *africana* and *melvillei*.

Length 1·5 mm.

Described from 1 ♀, holotype, as noted above. Presumably this species was obtained by Rust from the same host and locality as were the other specimens segregated by him under his number Z–15 and described by me as *T. africana*. According to Rust's slide labels, the specimens were reared from *Pseudococcus citri* collected at Durban, Natal, iii, iv, vi.1926.

2. **Tropidiophryne africana,** Compere (fig. 4).

Tropidiophryne africana, Compere, Univ. Calif. Publ. Entom., **5** (14), 1931, pp. 269–72.

Tropidiophryne melvillei, sp. n. (fig. 4).

The more important diagnostic characters have been given in the key.

♀. Mesoscutum, axillae, and scutellum submetallic dark bluish, in parts with traces of purplish ; tegulae and pronotum brownish, the collar of latter slightly bronzy. Head grading from semi-transparent brown to opaque brownish black with admixtures of bluish metallic and some faint purplish reflections, the bluish most extensive and pronounced across the face above sockets. Antennae brownish black to testaceous with some purplish ; metanotum and propodeum blackish. Sides and sternum of thorax mostly brownish black. Legs mostly dark brown grading in parts to testaceous except the fore coxae which are colourless.

Frontovertex slightly more than one-third the head width (5 : 13). (In *T. africana* frontovertex slightly less than one-third the head width (2 : 7).) Posterior ocelli separated from each other by more than twice the diameter of an ocellus.

Length 1·9 mm.

Unless mentioned otherwise, this species resembles *T. africana*.

Described from 5 ♀♀, holotype and paratypes, reared from a *Pseudococcus* sp. on *Aberia* by A. R. Melville, Scott Agricultural Laboratory, Nairobi, Kenya Colony, 3.vi.1937. Melville's No. C 138/40.

Genus **Microterys,** Thomson.

Key to the African Species of Microterys, *Females.*

1. Scape expanded and flattened below, from two to three times as long as wide. Scrobes wide and shallow, usually semicircular and broadly confluent above...3

Scape not expanded and flattened below, although the ventral margin may have a narrow, thin transparent keel at apex. Scrobes narrow and deep............2

2. Notum of thorax strongly convex, scutellum strongly convexly rounded from side to side and from base to apex, faintly reticulated. Forewings with two white cross-bands. General colour shining brown. Length 2·6 mm. (Kenya Colony)..1. *umbrinus*, sp. n.

Notum of thorax almost plane, scutellum with the disk almost flat, finely punctate reticulate, appearing granular. Forewings with one white cross-band. Mesoscutum purplish or greenish metallic, remainder of thorax and head mostly golden testaceous. Length 1·3 mm. (Kenya Colony, Natal, Transvaal)..2. **saissetiae,** sp. n.*

3. Forewings with one or two whitish cross-bands across the middle...............4

Forewings darkly infuscated from the base to near the apical margin, apical margin narrowly whitish. Scape widely expanded, less than twice as long as wide. Thorax testaceous to dark brown, mesoscutum and scutellum with metallic reflections (Natal)..................................3. *fuscipennis*, Compere

4. Forewings with two whitish cross-bands...5

Forewings with one whitish cross-band. Mesoscutum and scutellum testaceous brown, faintly metallic. Frontovertex one-fifth as wide as the head ; ocelli in a strongly acute angle (Kenya Colony).....................4. **kenyaensis** sp. n.*

5. Almost completely testaceous with the following parts more or less fuscous : concealed centre of pronotum, metanotum and centre of propodeum (Natal) 5. *nicholsoni*, sp. n.

Dominantly dark metallic with the following parts testaceous or brownish orange : head, collar of pronotum and sometimes mesopleura (Eritrea) 6. *bizanensis*, sp. n.

1. **Microterys umbrinus,** sp. n.

A large species, 2·6 mm. in length ; shining dark brown ; forewings with one white cross-band ; flagellum partly testaceous.

♀. General colour shining dark brown with admixtures of blackish near the margins of some sclerites ; head with very faint purplish lustre ; abdomen brownish black, submetallic ; distal half of funicle more or less testaceous and paler than remainder of flagellum which grades from dark brown to blackish ; legs varying shades of brown, the tarsi more testaceous. Tibiae of middle legs on dorsal aspect near base densely covered with short, soft, white hairs.

Head dorsal view, slightly more than twice as wide as long (28 : 13) ; frontovertex one-fourth head width, very finely rugoso-reticulate with feeble punctations. Ocelli in an acute triangle, the posterior pair about once their own diameter from the occipital margin and less than one-half their diameter from the orbits. Head frontal view, slightly wider than high (14 : 13) ; scrobes narrow, moderately deep, the outer margins carinated at meeting cheeks ; upper margins of antennal sockets slightly below the basal level of eyes. Face and cheeks sculptured similarly to frontovertex and clothed with very fine, inconspicuous setae. Eyes with sparse pubescence, appearing bare under low magnification.

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* Will be described fully in the Univ. Calif. Publ. Entom.

Scape cylindrical or nearly so, slightly thicker apically; pedicel slightly more than twice as long as wide and almost as long as first funicle joint (6 : 7); first funicle joint three and one-half times as long as wide; funicle joints decrease in length and increase in width so that the sixth is about as long as wide and more than one-half as long as the first (4 : 7); club slightly wider than the sixth funicle joint (5 : 4) and almost as long as the first two funicle joints; first two and sixth funicle joints with short coarse black setae; third, fourth and fifth funicle joints with soft pale setae.

Thorax strongly convex; scutellum strongly rounded from side to side and from base to apex, faintly longitudinally reticulate with sparse, fine, dark brown setae. Abdomen after shrinkage triangular, shorter than thorax; ovipositor slightly exserted.

Forewings less than two and one-half times as long as wide (7 : 3); centre of blade and extreme base darkly infuscated; clear hyaline below and the basal half of submarginal vein except at base; a moderately wide, even cross-band of soft white cilia extending in a slight arc from the apex of the postmarginal vein to the posterior margin of the blade; distad of the cross-band, the blade infuscated but not so darkly as across the middle; central infuscation partly interrupted below the middle by a narrow longitudinal pale streak which extends from the cross band to the outer margin of the speculum.

Length 2·6 mm.

Described from 4 ♀♀, holotype and paratypes. The specimen selected as holotype was received from Norman S. Noble, Department of Agriculture, New South Wales, under his number 15 and with the following data: " Ex *Ceroplastes* on coffee, Limuru, Kenya. 14–11–35." The 3 paratypes from the British Museum labelled as follows: " Ex *Ceroplastes destructor*, Limuru, Kenya Colony. 5–XII–1935, H. Wilkinson."

2. Microterys saissetiae, sp. n.

Microterys saissetiae, Compere, Univ. Calif. Publ. Entom. (In press.)

A single female reared from *Saissetia nigra*, collected by R. H. Le Pelley at Kiambu, Kenya Colony, v.1931, " No. 481 ex No. 408 is identified as *M. saissetiae*."

In the specimens of the type series the mesoscutum is dominantly purplish and in the specimen from Kiambu it is dominantly greenish.

3. Microterys fuscipennis, Compere.

Microterys fuscipennis, Compere, Univ. Calif. Publ. Entom., **4** (8), 1928, pp. 217–18.

4. Microterys kenyaensis, sp. n.

Microterys kenyaensis, Compere, Univ. Calif. Publ. Entom. (In press.)

5. Microterys nicholsoni, sp. n.

♀. The balsam-mounted representatives of this species are dominantly pale orange-yellow to pale brownish yellow; integument mostly semitransparent; mesoscutum faintly shining; abdomen across the base narrowly dark metallic. The following parts more or less fuscous: centre of pronotum, metanotum, propodeum, dorsum and sides of abdomen, ventral margin of scape, sixth funicle joint and club, distal tarsal joints of the fore and hind legs. First four and the sixth funicle joints with coarse, short black setae, fifth funicle joint white with pale setae. All coxae slightly suffused with dusky.

Frontovertex slightly less than one-third head width (3 : 10); ocelli in an acute angle, posterior pair about one-half their own diameter from eyes and about once their own diameter from occipital margin. Sculpture not visible in balsam ; fine brown setae visible along the inner orbits and some slightly coarser and darker on occipital margin. Scrobes wide and shallow, broadly confluent above and semicircular. Scape flattened and expanded below toward apex, about twice as long as wide ; pedicel less than twice as long as wide (5 : 3) ; first funicle joint as wide as long, plainly shorter than the pedicel (3 : 5) ; sixth funicle joint slightly wider than long (5 : 4) and about as long as the first ; club about as long as the distal three funicle joints and slightly wider than the sixth. All funicle joints of approximately equal length and all slightly increase in width distally.

Forewings slightly more than twice as long as wide (11 : 5) ; partly infuscated with two whitish cross bands beyond the stigmal vein.

♂. General colour dark metallic, frontovertex, face and cheeks more or less bluish green ; scape pale yellowish white, flagellum testaceous with some dusky suffusions ; legs mostly testaceous, middle and hind coxae more or less fuscous ; hind tibiae suffused with fuscous distad of the middle ; distal tarsi of forelegs and distal two or three tarsal joints of hind legs slightly fuscous.

Antennae with slightly curved setae of moderate length, not arranged in whorls. Scape slightly longer than the pedicel and first funicle joint combined ; pedicel about as long as wide ; first funicle joint three times as long as wide, the second about subequal, the increase in width and decrease in length hardly perceptible ; sixth funicle joint a trifle longer than wide (7 : 6) and more than one-half as long as the first (7 : 12) ; club about as long as the pedicel and first funicle joint combined and slightly wider than the sixth.

Described from 8 ♀♀ and 8 ♂♂, holotype, allotype, and paratypes, all mounted in balsam ; 7 ♀♀ reared from *Saissetia perseae*, Brain ; 1 ♀ ex *Coccus hesperidum*, Linn. ; 3 ♂♂ ex *S. perseae* ; 4 ♂♂ ex *Saissetia oleae* (Bern.). This material was collected by E. W. Rust at Durban and Congella, Natal, x, xi.1925. The holotype and allotype were collected at Congella and are from *S. perseae*.

Named after Dr. A. J. Nicholson, Division of Economic Entomology, Council for Scientific and Industrial Research, Canberra, Australia.

6. **Microterys bizanensis**, sp. n. (fig. 5).

♀. Head mostly testaceous with dark brown suffusions on cheeks near mouth. Notum of thorax and abdomen mostly blackish brown ; collar of pronotum testaceous ; mesoscutum and scutellum with slight bluish green and purplish reflections ; tegulae testaceous basally and fuscous apically ; axillae brownish black ; metanotum and propodeum black ; pleura of thorax testaceous to dark brown. Legs pale brownish yellow to dark brown, tibiae of middle legs and femora and tibiae of hind legs dark brown. Ventral margin of scape blackish ; pedicel and first four funicle joints testaceous brown ; fifth funicle joint yellowish white ; sixth funicle joint and club blackish.

Head dorsal view, about twice as wide as long ; frontovertex slightly longer than wide (6 : 5) and slightly less than one-third as wide as the head ; finely punctate-reticulate with very faint setiferous punctations ; ocelli in an obtuse triangle, the posterior pair further apart than from the anterior ocellus ; posterior pair less than one-half their own diameter from the eyes and slightly more than their diameter from the occipital margin. Head frontal view, slightly wider than high, antennal sockets below the basal ocular line.

Scape expanded below, about twice as long as wide ; pedicel about twice as long as wide and slightly longer than the first funicle joint ; all funicle joints about equal in length and slightly increasing in width distally, the first slightly longer than wide and the sixth slightly wider than long ; club about as long as the distal three funicle joints combined and about one and one-fourth times as wide as the sixth.

Notum of thorax moderately convex.

Wings as shown in fig. 5.

♂. Frontovertex, face, and cheeks metallic bluish green grading to brown near the mouth ; mesoscutum and scutellum brownish black with purplish and bluish green reflections, the latter dominant ; remainder of head and body blackish to brown ; antennae testaceous with the flagellum somewhat dusky. Legs pale yellowish white except the femora and tibiae of hind legs which are mostly fuscous.

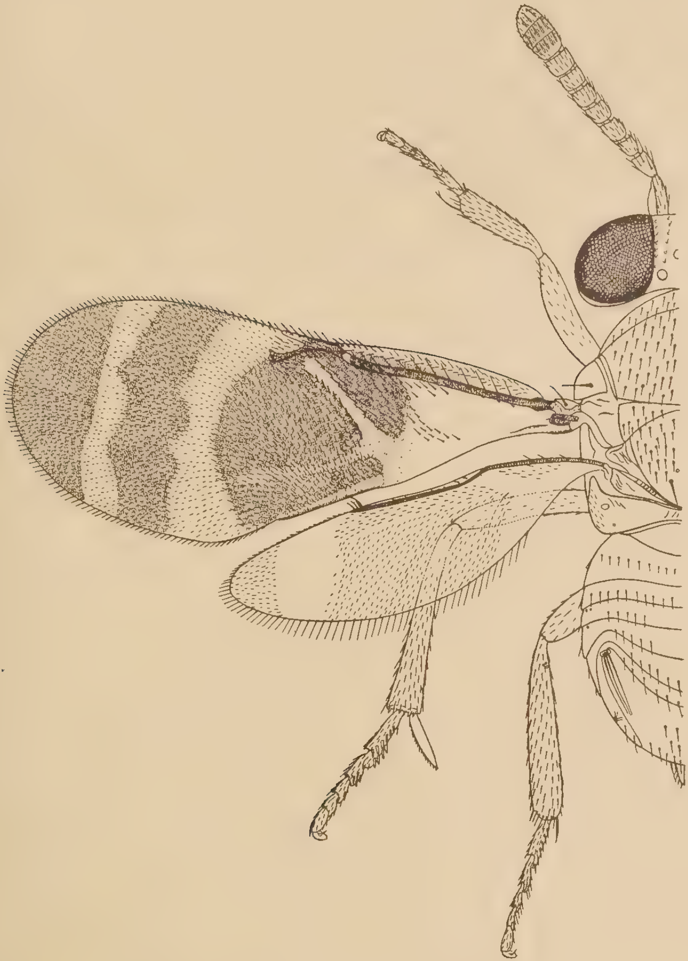

Fig. 5. *Microterys bizanensis* sp. n., ♀.

In the male sex this species greatly resembles *Microterys nicholsoni* ; the most conspicuous difference is that in this species the hind femora and tibiae are fuscous except the ends, while in *M. nicholsoni* the hind tibiae are suffused with fuscous distad of the middle.

Length 1·3 mm.

Described from 14 ♀♀ and 6 ♂♂, holotype, allotype, and paratypes, reared from *Saissetia cuniformis*, Leon., on *Schinus molle* and *Olea chrysophylla* collected at Nefasit, Asmara, and Mt. Bizan Monastery, Eritrea, iii, iv.1930, by H. Compere.

Genus **Bothriophryne,** Compere.

Bothriophryne Compere, Bull. Ent. Res. **28** (1), 1937, pp. 45–47.

In this paper three species are described as new and Mercet's species *tenuicornis*, described under *Trichomasthus*, Thomson, is transferred to *Bothriophryne.* The following brief characterization of *Trichomasthus* comparative to *Bothriophryne* is based on the study of a specimen determined by Mercet as *T. cyaneus* (Dalman), the genotype, and the species of *Bothriophryne* described by me. The species *tenuicornis* is known to me from the description only and I am not sure that it is in entire accord with the generic diagnosis given here, since some of the characters used by me are not included in Mercet's description. The new species *fuscicornis* agrees closely with all the characters given by Mercet in his description of *tenuicornis*, except the colour. In fact, *fuscicornis* may eventually prove to be a synonym of *tenuicornis*.

Key for Separation of Trichomasthus *from* Bothriophryne.

Head, dorsal view, menisciform, the anterior margin evenly gently convex without an abrupt median indentation ; twice as wide as long ; rugoso-reticulate with setiferous punctations that disappear or almost disappear on the face and cheeks. Head, frontal view, as wide as high ; antennal sockets with their upper margins about level with the basal ocular line ; scrobes shallow, short, semicircular above. Basal funicle joints not much longer than the pedicel... *Trichomasthus*, Thomson

Head, dorsal view, with the anterior margin abruptly and deeply indented in the middle, the narrow, highly raised area between the scrobes plainly visible ; usually about three times as wide as long ; rugoso-reticulate with coarse punctations on frontovertex, face and cheeks. Head, frontal view, usually slightly wider than high (15 : 13) ; antennal sockets with their basal margins usually well above the level of the basal ocular line. Scrobes short and deep, the inner sides vertical or nearly so, slightly convergent and separated by a high narrow ridge. Basal funicle joints three or four times as long as wide and much longer than the pedicel. Thorax much more convex than in *Trichomasthus* and the abdomen more elongate.................*Bothriophryne*, Compere

Key to the Species of Bothriophryne, *Females.*

1. Flagellum entirely dark brown or blackish. Mesoscutum with white setae......2
Flagellum with some joints pale yellow or whitish. Mesoscutum with brownish setae 3

2. Head indigo-blue with violaceous reflections. Pronotum and mesoscutum deep violet. Scutellum almost black, the sides and apex golden greenish. Pleura violaceous ; abdomen blue with the sides of the basal segment golden greenish (Egypt)...1. *tenuicornis* (Mercet)

Head bluish green with admixtures of purplish. Pronotum and mesoscutum almost black with faint bluish green and purplish reflections. Scutellum greenish black with cupreous or golden reflections on the disk. Pleura black. Abdomen mostly black metallic, the basal segment strongly greenish (Cape Province, Natal)...2. *fuscicornis*, sp. n.

3. Head in dorsal view about three times as wide as long. Frontovertex slightly wider than long (6 : 5).. 4

Head in dorsal view slightly more than twice as wide as long (11 : 5). Frontovertex as wide as long. Antennal club fuscous ; distal funicle joints yellowish white (Tanganyika)...3. *dispar*, sp. n.

4. Antennal club fuscous, distal one or two funicle joints yellowish white. Scutellum bluish green apically and purplish basally. Frontovertex and face bluish with strong purple admixtures (Natal).........4. *purpurascens*, sp. n.

Antennal club whitish, concolorous with the preceding joint. Scutellum entirely bluish green. Frontovertex dominantly bluish green, the face less refringent and with purplish admixtures (Uganda)........................5. *ceroplastae*, Compere

1. **Bothriophryne tenuicornis** (Mercet).

Trichomasthus tenuicornis, Mercet, Bull. Soc. Roy. Ent. Égypte, **9,** 1925, p. 44.

Aside from colour the characters mentioned by Mercet are those common to all the species of *Bothriophryne.* Mention is made of coarse punctations on the frontovertex and small white hairs on the face. If the face is not coarsely punctate this character will readily distinguish this species from the others described here. The antennae are described as inserted at the level of the base of the eyes. Under " observations " Mercet stated that this species can be easily distinguished from all other species of *Trichomasthus* by the long slender antennae with the basal joints of the funicle three or four times as long as wide.

Length 2·7 mm.

Mercet's specimens were reared from *Ceroplastes africanus*, Green, infesting *Albizzia lebbek*, collected in Egypt.

2. **Bothriophryne fuscicornis,** sp. n.

This species can be separated from those that follow by the uniformly fuscous flagellum and the slightly flattened whitish setae on the mesoscutum.

♀. General colour black metallic. Frontovertex, face and cheeks greenish blue with admixtures of purplish, the latter most pronounced on the face. Mesoscutum faintly greenish to purplish on a blackish ground. Axillae blackish. Scutellum greenish black with some admixture of cupreous on the disk. Sides of propodeum and abdomen across the base highly refringent metallic greenish. Metanotum, propodeum except sides, pleura and sternum of thorax, and all coxae and femora mostly blackish, the latter with a pronounced pale annulus near base. Tibiae of middle and hind legs yellowish white, the base of the latter fuscous ; remainder of legs light brown. Scape light brown, pedicel and flagellum blackish.

Head dorsal view, three times as wide as long ; frontovertex slightly wider than long (9 : 7) ; ocelli in a strongly obtuse angle, the posterior pair separated from the orbits and occipital margin by less than one-half their own diameter. Scape slightly thickened apically, slender and cylindrical near base, slightly longer than the first funicle joint. Pedicel longer than wide (4 : 3) and less than one-half as long as the first funicle joint. First funicle joint three times as long as wide, the succeeding joints decreasing in length so that the sixth is one and one-half times as long as wide and almost imperceptibly wider than the first ; club slightly less than twice as long as wide (9 : 10), slightly wider than the preceding joint (5 : 4), and about as long as the first funicle joint.

Abdomen long and slender pointed at the apex ; ovipositor shortly exserted. A specimen mounted in balsam, when fresh and not distended by pressure of the cover slip, measures 3·3 mm. in length and the abdomen inclusive of the ovipositor is about as long as the head and thorax united.

The wings are typical. Marginal vein about as long as wide ; postmarginal vein short, about one-half as long as the stigmal, and not reaching as far apically.

Except for *Bothriophryne tenuicornis* (Mercet), the male of which is unknown but presumably shares the character with the female, this species in the male as well as the female sex can be distinguished by the white setae on the mesoscutum.

♂. In colour very much like the ♀. Mesoscutum blackish without greenish and purplish reflections ; scutellum slightly less greenish than in the female. Middle and hind tibiae whitish and the middle femora with a very distinct annulus near base.

The proportions of the antennal joints are quite similar to those of the female, although in this sex the flagellum is covered with numerous, long, curved setae. Scape one and one-third times as long as the first funicle joint ; pedicel one and one-half times as long as wide ; first funicle joint almost four times as long as wide, the sixth about one-half as long as the first , club not quite as long as the first funicle joint.

Length 1·7 mm.

Described from 14 ♀♀ and 4 ♂♂ holotype, allotype and paratypes, reared from a *Ceroplastes* sp. (No. 11936) on wild *Acacia* sp., Waterval Ranch, Villiersdorp, Cape Province, South Africa, 26.xi.1936, by H. Compere.

What appears to be the same species was reared by E. W. Rust from *Ceroplastes* sp. (questionably *longichoda*, Brain) collected at Durban and Umbilo, Natal, x.1925. In the Natal samples the dorsum of the head is dominantly purplish. In the type specimens the dorsum of the head is dominantly bluish green.

3. **Bothriophryne dispar,** sp. n.

The single specimen of this species appears slightly more robust but this effect may be the result of shrinkage. The head is rigid so that the proportions given are considered reliable. Whether the abdomen is as long as the head and thorax united cannot be ascertained with certainty owing to distortion after drying.

♀. Frontovertex bluish green with a black ground ; face and cheeks less bluish green and rather generally violaceous with a black ground. Scape light brown ; pedicel, first four funicle joints and one-half of the fifth, and club dark brown to blackish ; apical half of fifth and the sixth funicle joint pale brownish yellow. Mesoscutum black suffused with bluish green and violaceous. Axillae black. Scutellum greenish with some cupreous and golden reflections. Sides of propodeum and abdomen across base highly metallic greenish. Sides and sternum of thorax, coxae, and most of femora blackish to dark brown. Middle and hind tibiae yellowish white, the latter only slightly fuscous near the base. Distal ends of femora, annulus near base of middle femora, front tibiae, and most of the tarsi pale brownish yellow to yellowish white.

Head dorsal view, slightly more than twice as wide as long (11 : 5). Frontovertex as wide as long and a trifle more than one-third the head width. Ocelli in a strongly obtuse angle, the posterior pair about one-half their own diameter from orbits and occipital margin, the median ocellus about as far from the non-punctate integument of the scrobes as from the occipital margin. In this specimen the punctations appear slightly less coarse than in the other species. Antennae inserted above the basal ocular line by the length of a socket. In the other species the antennae inserted a trifle lower, but by actual measurement the difference is only one-third or one-fourth the length of a socket.

The antennal portions do not appear unlike those of the preceding species, nor do the wings present any distinctive characters not shared by the other species.

Length, 1·9 mm.

Described from 1 ♀, holotype, reared from a *Ceroplastes* sp. collected by D. Vesey Fitzgerald, Mafia Island, Tanganyika, 1936.

4. **Bothriophryne purpurascens,** sp. n.

Morphologically this species does not appear greatly unlike *Bothriophryne fuscicornis*. It is, however, rather strikingly different in colour.

♀. Frontovertex strongly purplish with some greenish blue, face and cheeks less brilliant. Antennae as in *Bothriophryne dispar*, the sixth and apical half of fifth funicle joints yellowish in contrast to the dark brown to fuscous club, pedicel, first four, and basal half of the fifth funicle joints. Mesoscutum more strongly flushed with bluish green and purple than in the other species. Scutellum vivid bluish green apically, grading to purplish basally.

Frontovertex slightly narrower than in *Bothriophryne fuscicornis* ; in the latter it is slightly wider than long (9 : 7) while in this species it appears as wide as long. The differences are slight and there is considerable chance for error in attempting to make precise comparative measurements such as these.

Length, 2·7 mm.

♂. Colour similar to that of the females and structurally similar to males of the other species.

Length, 1·7 mm.

Described from 11 ♀♀ and 4 ♂♂, holotype, allotype, and paratypes, found in a vial among E. W. Rust's unmounted specimens. These specimens were numbered S–18 by Rust. In Rust's slide-mounted collection the identification number S–18 is given to a species of *Trichomasthus* reared from *Saissetia persimilis*, Brain. Under Rust's No. S–22 are 3 ♀♀ and 3 ♂♂ which appear indistinguishable from the unmounted specimens labelled S–18 and described as *Bothriophryne purpurascens*. The specimens mounted on slides with the No. S–22 bear the following data : " Ex *Ceroplastes* on custard apple, Congella, Natal, 23.ii.1926, Rust."

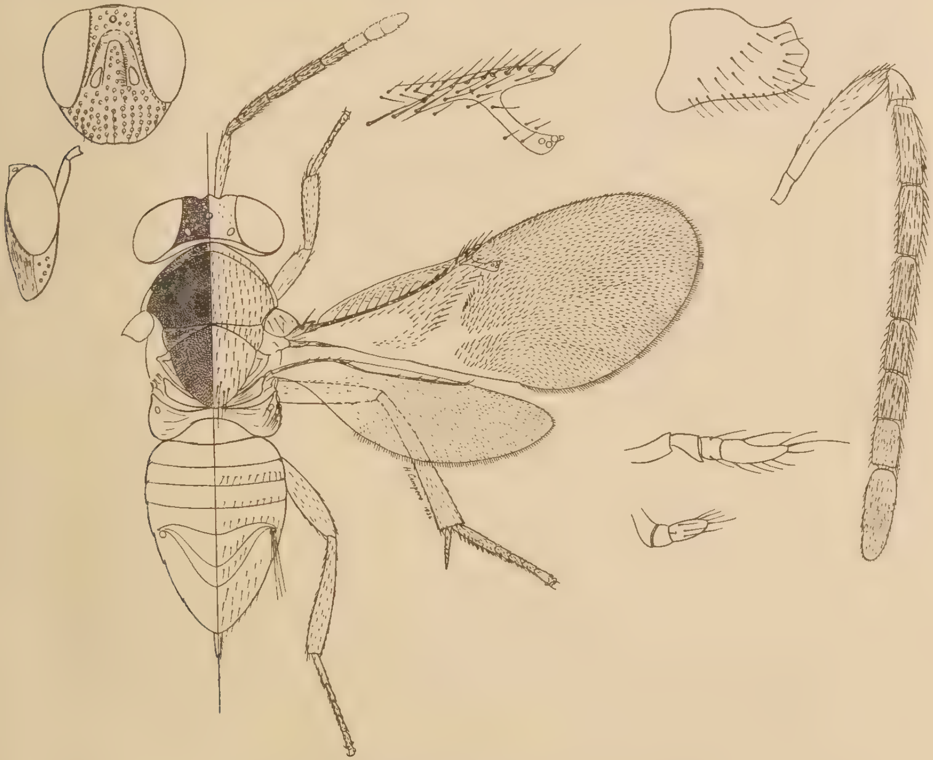

Fig. 6. *Bothriophryne ceroplastae*, Compere, ♀.
(After Compere, Bull. Ent. Res., **28**, 1937, p. 45 ; drawing retouched.)

5. **Bothriophryne ceroplastae,** Compere (fig. 6).

Bothriophryne ceroplastae, Compere, Bull. Ent. Res., **28** (1), 1937, pp. 45-47.

The figure given here was previously published in the Bulletin of Entomological Research. The drawing has been retouched by making some of the lines heavier.

Genus **Leptomastix,** Förster.

Leptomastix bifasciatus, Compere.

Leptomastix bifasciatus, Compere, Bull. Ent. Res., **29** (3), 1938, pp. 323–24.

The original description reads, " The two longitudinal bands on the forewings distinguish this species." This character was used in the key to the African species of *Leptomastix* for the identification of *L. bifasciatus*. The acquisition of additional specimens of *Leptomastix* from Kenya and Uganda with faintly marked or partly absolute bands on the forewings and with different colour markings makes the identification of this species difficult.

The holotype was reared from a *Pseudococcus* sp. collected at Uitenhage, Eastern Province, Cape of Good Hope. In the Uitenhage specimens the longitudinal bands are very distinct. The first band parallels the anterior margin from the middle of the submarginal vein to near the extreme apex of the blade. The second band commences near the base of the speculum and extends to slightly below the extreme apex of the blade. A typical wing with distinct bands is shown in the figure previously published.

The following specimens are identified as *Leptomastix bifasciatus* although it is by no means certain that these samples are all representatives of one species.

2 ♀♀, " Kitito, Kenya Colony, 23.x.1931, H. C. James. No. 4, ex pupae among mealybugs on *Combretum splendens*."

In these specimens the anterior band is distinct and the second band almost obsolete, its presence barely indicated in the centre of the blade. They differ from the type specimens in having the axillae and a large part of the mesoscutum flushed with fuscous. Except for narrowly around the margins the sides of the mesoscutum are testaceous.

5 ♀♀ and 3 ♂♂, Nyali Coast, Kenya Colony, 11.viii.1937, A. R. Melville, collector. No. C–189.

In the female sex the second longitudinal band is absent or nearly so. In colour the Nyali Coast samples are quite similar to the type specimens.

The males are quite similar to the females in colour.

Genus **Neodiscodes,** Compere.

Neodiscodes martinii, Compere.

Neodiscodes martinii, Compere, Univ. Calif. Publ. Entom. **5** (14), 1931, pp. 272–74 ; Proc. Haw. Ent. Soc. **9** (3), 1937, pp. 285–86.

Among the parasites reared by Melville are 4 ♀♀ and 1 ♂ *Neodiscodes* under two identification numbers ; 2 ♀♀ were reared from a *Pseudococcus* sp. collected at Kilifi, Kenya Colony, by Melville 13.viii.1937, and bear his number C-199 ; 2 ♀♀ and 1 ♂ were included in the same series as *Tropidiophryne melvillei* and bear data " Ex C79 on Kei apple, S.A.L. 139 and 140."

The specimens from Kenya have the frontovertex less coarsely punctate than do the type specimens of *Neodiscodes martinii* collected in Eritrea. In my opinion the Kenya samples are not specifically different.

Genus **Leptomastidea**, Mercet.

Leptomastidea jeanneli, Mercet.

Leptomastidea jeanneli Mercet, Bol. Real Soc. Esp. Hist. Nat., **24**, 1924, pp. 254–56.

3 ♀♀ and 1 ♂ reared from *Pseudococcus kenyae*, Le Pelley, collected in Kenya Colony at Kasarini Kiambu, 19.iv.1937 and 3.v.1937, and bearing A. R. Melville's numbers C148 and C151, are identified as *Leptomastidea jeanneli*, Mercet. In the collection of the Citrus Experiment Station is a single female reared from a *Pseudococcus* on *Olea chrysophylla* at Nefasit, Eritrea, 14.v.1930, which is also identified as *L. jeanneli*. None of these specimens is in entire accord with Mercet's description, nor is the Eritrean sample exactly like the Kenya samples.

In his description of *Leptomastidea jeanneli*, Mercet states that the legs are brownish yellow with the middle and hind femora whitish yellow, as are the tarsi. In contradiction the figure shows the hind femora blackish in marked contrast to the generally light colour of the remainder. In Mercet's key to the species *L. jeanneli* is characterized by having the intermediate crossband on the forewing entire.

Except for a narrow interruption of the intermediate crossband posterior of the middle, the Eritrean specimen seems in agreement with most of the description, exclusive of the legs. In leg coloration this specimen agrees with the figure, as the hind femora are blackish.

The Kenya samples collected by Melville have the frontovertex yellow ; face, ventral half of scape, apex of pedicel, prepectus, forelegs and an intrusion on the mesopleura white. The posterior femora are fuscous dorsally.

The specimens described by Mercet are recorded as having been collected at Naivasha in Uganda. This is a mistake, for Naivasha is in Kenya Colony.

Genus **Cheiloneurus**, Westwood.

Cheiloneurus carinatus, Compere.

Cheiloneurus carinatus, Compere, Bull. Ent. Res. **29** (3), 1938, pp. 330–332.

4 ♀♀, 1 ♂, ex *Pseudococcus* sp., Kilifi Coast, Kenya Colony, 13.viii.1937, A. R. Melville collector ; ♀♀ No. C196, ♂ No. C197.

The male is similar to the allotype collected in Eritrea. In the female sex the concealed part of the pronotum is blackish, collar silvery, and the remainder golden testaceous ; anterior half of mesoscutum, axillae and scutellum golden testaceous ; mesopleura partly golden testaceous, pedicel and first four funicle joints partly fuscous, the fifth and sixth testaceous.

3 ♀♀ ex mealybug material on yam leaves, Njala, Sierra Leone, 3.ix.1936, E. Hargreaves collector.

These are somewhat darker coloured than the Kilifi Coast specimens. The blackish on the pronotum is more extensive, spreading to the collar ; axillae and scutellum with slight suffusions of fuscous in parts ; mesopleura dark greenish blue with some purplish.

Cheiloneurus cyanotus, Waterston.

Chiloneurus cyanotus, Waterston, Bull. Ent. Res., **7** (3), 1917, pp. 247–49.

Cheiloneurus cyanotus, Compere, Bull. Ent. Res. **29** (3), 1938, pp. 333–34.

4 ♀♀, " Ex *Ceroplastes angolensis*, Ruiru, Kenya Colony, 6.i.1937, A. R. Melville, No. C105."

The specimens of this sample have the first five funicle joints white, the sixth blackish and are similar to sample III mentioned in the preceding paper.

3 ♀♀, " Ex *Chilocorus distigma*, Newala, Tanganyika T., 2.xi.1936, D. V. Fitzgerald, Nos. 5359-B, C.D."

ECOLOGICAL NOTES ON THE *SIREX* WOOD WASPS AND THEIR PARASITES.

By H. S. Hanson.

Farnham House Laboratory, Imperial Institute of Entomology.

(Plates I–VI.)

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1. Introduction.

The following notes on the ecology of the *Sirex* wood-wasps and their parasites have been collected during a period of several years. In 1927 the Imperial Institute of Entomology received a request from Dr. David Miller, Government Entomologist of New Zealand, for parasites for the control of *Sirex noctilio*, a species of wood-wasp which had become established in New Zealand and was rapidly increasing in the coniferous forests in that country.

The preliminary investigations were carried out by Dr. J. G. Myers, of Farnham House Laboratory, in collaboration with Dr. R. N. Chrystal, of the Imperial Forestry Institute, Oxford. While the investigations were in their early stages Dr. Myers left Britain to take up duties in Trinidad in 1928. After that date all subsequent investigations on behalf of the Imperial Institute of Entomology were carried out by the present writer under the direction of Dr. W. R. Thompson, Superintendent of Farnham House Laboratory. Dr. Chrystal carried out entirely independent biological investigations at Oxford. The results of his researches and those of Dr. Myers have been published in a series of papers.

The large-scale operations carried out on behalf of Farnham House Laboratory afforded exceptional facilities for the study of the ecology of the wood-wasps and their parasites, and much useful information about their inter-relationship was collected. It is felt that the publication of the data is desirable in order to supplement what has already been written on the subject.

2. Duration of the Life-cycle of the Sirex Wood-wasps and their Parasites.

The *Sirex* wood-wasps are probably familiar to all those who are interested in the study of nature. Four species normally occur in Britain : *Sirex gigas*, L., *S. cyaneus*, F., *S. noctilio*, F., and *S. juvencus*, L. Other species are sometimes introduced in imported timber, but have not been recorded as breeding species.

In a paper by Dr. R. N. Chrystal (1928) the late Dr. James Waterston gave some systematic notes on British wood-wasps. These notes should be consulted by those interested in the determination of the various species.

Sirex gigas, L., is a very conspicuous yellow and black insect, while the other three species are all of a dark metallic blue colour and are very similar in general appearance. Formerly all three blue wood-wasps were known to foresters and others generally interested in forest insects as *Sirex juvencus*, L., but Dr. Waterston has shown that the blue wood-wasp most common in Britian is *Sirex cyaneus*, F., and that *Sirex juvencus*, L., and *Sirex noctilio*, F., are comparatively rare insects.

Sirex gigas and *S. cyaneus* occur in most coniferous woods throughout Britain but are never very numerous unless local conditions are exceptionally favourable for their increase. Both species are attacked by two Hymenopterous parasites, an Ichneumonid, *Rhyssa persuasoria*, L., and a Cynipid, *Ibalia leucospoides*, Hochenw. A brief outline of the life-cycle of these insects is given below.

(*a*). *Life-cycle of* Sirex.

The normal life-cycle of both *Sirex gigas* and *S. cyaneus* extends over a period of three years from the egg to the adult stage, but development is sometimes retarded and the adult insects may not emerge from the timber until several years have elapsed. Most coniferous timbers are used for breeding purposes, but perhaps silver fir, spruce, larch and pine are the most frequent hosts.

The eggs are laid during the summer from the end of June onwards, in a short oviposition hole in the outer layers of the wood. During the first winter the tiny larvae may be found burrowing in tunnels running almost at right-angles to the oviposition hole at first, later they begin to burrow deeper into the wood, and during the second summer they are often about 1½ inches below the surface ; as the larvae develop they burrow towards the pith, and during the second winter they may be found about half-grown. Plate I, fig. 1, shows half-grown *Sirex* larvae burrowing in the region of the pith in a small silver fir log during the second winter of their development. The larvae continue to burrow during the whole of the following summer, and as they become full-grown they turn outward and burrow towards the surface. During the third winter they are to be found lying full-grown in chambers near the surface of the wood ready to pupate (Plate I, fig. 2). The frass-filled burrows formed during the previous summer are shown in Plate I, fig. 3. The larvae pupate in the spring, usually from ½ to 2 inches below the surface of the wood. Plate II, fig. 1, shows a female *Sirex cyaneus* pupa in the pupal chamber.

In longitudinal section, the exit tunnel made by *Sirex cyaneus* is only slightly curved, while that of *Sirex gigas* is generally very strongly curved, describing almost a complete quadrant.

Plate II, fig. 2, shows a female *Sirex gigas* adult in the pupal chamber ready to emerge. The adult wood-wasps begin to emerge in June ; the males frequently emerge first, but are seldom seen after they leave the timber, as they spend most of their time among the crowns of the trees. The females are often seen ovipositing in logs or standing trees. Large, over-mature, standing trees which are slowly dying from the top downwards often support a colony of wood-wasps for a long period of years, the region of infestation increasing from year to year as additional portions of the tree become suitable for breeding purposes.

Two and sometimes three generations of *Sirex* larvae may be present in the same piece of timber. The length of the duration of the *Sirex* larval stage is of considerable importance as will be seen when dealing with the inter-relationship of the host and parasites and the percentage of parasitism.

Discussing the exit holes of *Sirex*, Dr. Chrystal states " J. H. Fabre in an essay entitled 'The Problem of *Sirex*' has described how in *S. augur* the larva, when full-grown, lies lengthwise in the tree not far from the centre of the trunk. In this position metamorphosis takes place and the adult insect, on emerging, is faced with the problem of cutting its way out through the wood in which it is a prisoner. In the vertical plane in which it lies this is a difficult task for the heavily armoured adult, which is incapable of bending the body freely. The task is accomplished, according to Fabre, by the construction of an exit gallery which is the wide arc of a circle whose lower extremity is connected with the larval tunnel, and whose upper extremity is prolonged in a straight line which ends at the surface with a perpendicular or slightly oblique incidence. The wide connecting arc, which enables the insect to adjust its position gradually, is a curve which Fabre has shown approximates as nearly as possible to the circumference of a circle, and the construction of which is a constant feature of the species even over lengths that sometimes exceed four inches. These remarkable observations by the great French naturalist have not been duplicated in the case of *Sirex cyaneus*."

The above remarks are quoted because of their general interest with reference to the difference in the shape of the exit tunnels formed by the various species of *Sirex*, and also because of their special interest in relation to problems of insect behaviour.

After discussing Fabre's description of the exit tunnel of *Sirex augur*, Dr. Chrystal described by way of contrast, the exit tunnel formed by *Sirex cyaneus*, and states that in nearly every case he examined " the pupal cell was so constructed that the adult was afforded a perfectly straight forward passage to the outside, whether it chose to proceed in an oblique or horizontal direction." He gives the average depth of the pupal chamber as being from $\frac{3}{4}$ to $\frac{1}{2}$ an inch, but says that in many cases, especially in male pupae, the pupal cell lies less than $\frac{1}{4}$ inch from the exterior. The present writer has noticed that *S. cyaneus* larvae seem to prefer the sapwood when burrowing in larch and the larval tunnel is in consequence generally near the surface. Plate V, fig. 3, shows the pupal chamber of *S. cyaneus* in larch timber with the remains of an adult female. This specimen was parasitised by *Rhyssa* and the full-grown parasite larva is seen *in situ*. When, however, *S. cyaneus* breeds in large silver fir, the larvae burrow to a considerable depth and the length of the exit burrow is correspondingly long. Examples are seen on Plate II, fig. 1, Plate IV, fig. 2, and Plate VI, fig. 2. In each case it will be seen that the tunnel is not perfectly straight, but shows a slight curve, although it bears no strong resemblance to the exit tunnel of *S. augur* as described by Fabre.

Dr. Chrystal's studies were confined almost entirely to *S. cyaneus* material, consequently he makes no reference to the shape of the exit tunnels of *Sirex gigas*, which differ considerably from those of *S. cyaneus* and bear a very strong resemblance to the tunnels of *S. augur* as described by Fabre, except that the upper extremity is not prolonged into a straight line. Two *Sirex gigas* exit tunnels are shown on Plate VI, fig. 1. It will be seen that each tunnel described a complete quadrant, although the angle of incidence with the surface of the timber is slightly different. The shape of these exit tunnels is typical for *S. gigas*. The photograph is of special interest because it shows two exit tunnels converging to one exit hole, a rather unusual occurrence. The *Sirex* adult from the lower tunnel emerged first, as is shown by the presence of the bark frass in the tunnel. In the absence of this exit hole the last half inch of the second *Sirex* tunnel would normally have been produced in an almost horizontal direction, but the tunnel is seen to be strongly curved downwards at this point, as if the insect had deliberately burrowed in that direction in order to avail itself of the existing exit hole. The explanation appears to be that the lower portion of the second *Sirex* tunnel would be the first point of intersection with the first tunnel, and as there would be a breach in the wall of the second tunnel formed at this point, the course of the insect would be automatically deflected owing to the peculiar manner in which the insect is propelled forward during the process of boring the tunnel. At the end of the last abdominal segment there is a long, pointed, spike-like process which is thrust against the side of the completed part of the tunnel and used as a lever to propel the body of the insect forward and thus assist the legs which are in a very cramped position within the narrow tunnel. This tail-like organ can be seen in Plate II, fig. 2. The pointed process is much more strongly developed in the female wood-wasp than in the male, and although it is much shorter than the ovipositor, like the latter organ, it differs in length in each of the British species. The last segment of the wood-wasp larva is also furnished with a sharp spike which is used in the same way. It is doubtful whether the insect would be able to bite its way through the wood without the assistance of this organ.

In his Presidential Address to the Entomological Society of London in 1932, Dr. H. Eltringham F.R.S., in discussing the insect's powers of biting its way through wood and even lead remarked : " This power of biting seems to cease on emergence into the open air, since a *Sirex* cannot, or at any rate does not, bite its way out of a match box."

It will be seen from what has been said, that when confined in a wooden box too large to allow this organ to be brought into use, the insect is unable to "keep its nose to the grindstone" and bite its way out, but it does not lose its power of biting.

In the previous quotation it is stated that the adult *Sirex augur* is faced with the " problem " of cutting its way out of the timber, and it is explained that in order to do so the insect described an arc, thus changing its position from a vertical to a horizontal plane. If the tree is felled the " problem " may be further complicated by the fact that the insect in the pupal chamber will then be in a horizontal position instead of vertical. The problem is, however, supposed to be solved in exactly the same way by all specimens of that particular species, except that in the case of a felled tree the exit tunnel will be bored only in a horizontal plane if the insect decides to emerge from the side of the log and vertically if it chooses to emerge from the upper side. This statement infers mental process and choice of course of action on the part of the insect, presumably based on a knowledge of its position relative to the shape of the tree and the position in which the latter may be either standing or lying. It is clear, however, that each individual *Sirex* adult must perform the task without any knowledge of the external shape or position of the object forming the medium in which it is boring.

Whether the pupal chamber of *S. augur* is actually formed lengthwise in the tree as described by Fabre, *i.e.*, in the direction of the long axis of the stem, and parallel with the pith and the bark, the present writer is not in a position to say, as he has no personal knowledge of the habits of this species, but this is certainly not the case with the pupal chambers of *S. gigas* and *S. cyaneus.* In both species the larvae turn outwards towards the bark as seen in Plate I, fig. 2, and the greater part of the curved exit tunnel is bored by the full-grown larva before the pupal stage is reached. Plate II, fig. 1, shows a female *S. cyaneus* pupa in the pupal chamber. Plate IV, fig. 1, shows a *S. gigas* pupal chamber containing a *Rhyssa* pupa. In the case of *S. cyaneus* the larva often turns outward at a distinct angle, as seen in Plate IV, fig. 2, but

S. gigas generally forms a definite curve. It will be seen, therefore, that in these two species the adult insect is not confronted with the problem of getting from a vertical to a horizontal position, as the greater part of the task has been performed by the larva. It may, however, be argued that this is merely handing the problem back a stage to the larva for solution, and that the case for mental process is all the more complex, since the larva has not only to solve the geometrical exit problem, but has also to visualise the future requirements of the heavily chitinised adult insect. The writer does not consider that Fabre actually attributed reasoning powers to the insect and he personally is convinced that no such mental process is involved and the process is entirely a mechanical one. Plate I, figs. 1 and 3, show that during the feeding stage the larvae wander at random through the timber, the rate of their forward progress being determined by their food requirements. During this period it is essential that the timber be gnawed into very tiny particles in order to obtain the food on which the larva subsists. This would be facilitated by gnawing at the ends of the long fibres in the wood rather than by biting off splinters from the sides of these fibres. When, however, the feeding period is finished and the only remaining urge is the formation of a chamber in which to lie, biting off tiny particles is no longer absolutely necessary, and as boring is now the only task, the act of biting off larger particles of the long fibres tends to turn the tunnel in a transverse direction as the tunnel is more easily enlarged when working across the grain of the timber. By the time the resting chamber has reached the required dimensions the tunnel has assumed the shape of a curve, after pupation a continuation of this curve, or even a straight tunnel, will bring the insect to the surface.

If the above explanation is correct, it will probably be found that the greater part of the curved portion of the exit tunnel of *Sirex augur* is formed by the larva and not by the adult insect as stated by Fabre.

Scheidter (1923) states that in Germany, *S. gigas* and *S. augur* attack the biggest stems, whereas *S. juvencus* and *S. noctilio* prefer poles, probably because their short ovipositors cannot pierce thick bark ; *S. augur* pupae were found at a depth of 4¾ inches from the surface. Dissections showed that females of *S. augur* contain an average of over 1,000 eggs each. In *S. noctilio* the number is about 400. Dissections made by Dr. Chrystal indicate that the number of eggs in *S. cyaneus* is between 300 and 400 on an average.

(*b*). *Life-cycle of* Ibalia leucospoides, *Hochenw.*

The biology and post-embryonic development of *Ibalia leucospoides* have been described in great detail by Dr. R. N. Chrystal (1930).

The observations of the present writer confirm those of Dr. Chrystal, so far as the life-cycle of *Ibalia* is concerned, but his conclusions as regards the relative efficiency of this parasite as compared with *Rhyssa*, and their inter-relationship with the host, differ considerably. This subject will be discussed in detail later. Only an outline of the life-cycle of *Ibalia* will be given here ; the reader is referred to Dr. Chrystal's excellent paper for a full description of the insect and its biology.

The life-cycle of *Ibalia* extends over a period of three years. The *Ibalia* adults begin to energe towards the end of July, but are most numerous in late August and early September. At this time they may be seen ovipositing in trees in which *Sirex* have recently oviposited.

The ovipositor of *Ibalia* does not project beyond the end of the abdomen, as is the case in many other Hymenopterous parasites, but lies coiled within the body. The insect is highly specialised and is unable to attack the host larva by boring through the bark and timber. The oviposition hole of *Sirex* has first to be located, *Ibalia* then lowers her ovipositor into the *Sirex* oviposition hole and inserts her eggs within the eggs or recently hatched larvae of *Sirex*. Each *Ibalia* larva develops as an internal parasite until the third larval stage is reached. When more than one parasite larva is present the supernumerary larvae are destroyed at this stage, and the survivor then emerges and devours the remains of the host larva ; this period of development as an internal parasite occupies about two years. After emerging from the *Sirex* larva during the second summer, the *Ibalia* larva remains as a fourth-stage larva within the *Sirex* tunnel until the spring of the following year. It then pupates and emerges from the tree. The adult insect bores an exit hole through the timber and bark. It has been mentioned that *Sirex* larvae normally burrow towards the pith during the first year of their development, but when *Sirex* larvae have been parasitized by *Ibalia* they do not follow the normal course ; at first they begin to burrow into the timber, but as the parasite begins to develop the *Sirex* larva changes its course and tends to burrow outwards towards the bark, so that the tunnel formed by a parasitized *Sirex* larva is much nearer the surface than that of an unparasitized larva. Plate III, fig. 1, shows three *Sirex* tunnels, two of which represent the normal course of unparasitized *Sirex* larvae and one which shows the course taken by a *Sirex* larva parasitized by *Ibalia.* In this case, however, all three *Sirex* larvae have been parasitized by *Rhyssa* when they were one year old. Plate III, fig. 2, shows the tunnels of three *Sirex* larvae which were parasitized by *Ibalia.* Two of these tunnels contain fourth-stage *Ibalia* larvae resting during the third winter ready to pupate in the spring. The one in the centre contains a *Rhyssa* larva showing that one of the three original *Ibalia* larvae was subsequently parasitized by *Rhyssa.*

(*c*). *Life-cycle of* Rhyssa persuasoria, *L.*

The life-cycle of *Rhyssa* is completed in one year. The adults begin to emerge in the spring and may attack the host larvae at any time throughout the summer, as, unlike *Ibalia,* they do not attack the eggs and first stage larvae of the host, but locate the *Sirex* larvae which have completed one or more years development. Having located the position of the *Sirex* larva by means of the antennae, *Rhyssa* proceeds to bore a hole with her ovipositor, penetrating the bark and timber until the host larva is reached. The egg is then laid upon the host larva within its tunnel. The statement still repeated by some authors, that *Rhyssa* sometimes reaches its host by inserting its terebra along the burrows of the latter, is incorrect.

As *Sirex* normally takes three years to complete its development, it will readily be seen that one generation of *Sirex* may produce three generations of *Rhyssa.* This subject will be referred to again when discussing the inter-relationship of the host and its parasites. Plate III, fig. 1, shows the first generation of *Rhyssa* which are the result of *Sirex* larvae being parasitized when one year old. Plate III, fig. 2, shows a *Rhyssa* larva of the second generation, as although the host in this case was *Ibalia* it corresponds to a *Sirex* larva two years old. Plate III, fig. 3, also shows a *Rhyssa* larva of the second generation. In this case the host was a *Sirex* larva, two years old, which would normally have spent the winter as a full-grown larva and emerged as an adult in the following summer.

The discrepancy in the size of the *Rhyssa* larvae is due to the size of the host. One-year-old *Sirex* larvae and *Ibalia* larvae produce very small *Rhyssa* adults, while two-year-old *Sirex* larvae produce fairly large *Rhyssa*, and full-grown *Sirex* larvae produce very large *Rhyssa.*

Plate IV, fig. 1, shows the pupa of a third generation *Rhyssa.* In this case the host was a full-grown *Sirex* larva which was in the pupal chamber ready to pupate. Plate IV, fig. 2, shows an adult female *Rhyssa* tunnelling the exit hole from pupal chamber of *Sirex.* When the *Sirex* infested logs are very large the *Sirex* larvae may be out of reach of *Rhyssa* during the second summer, but when the timber is under 3 inches in diameter the *Sirex* larvae are within reach of large specimens of *Rhyssa* during the whole period of their development and in such cases parasitism by *Rhyssa* is very high and few *Sirex* escape destruction.

Even in the third year, when *Sirex* has completed its development and is about to emerge, the adult insect is often parasitized by *Rhyssa* while actually burrowing the exit tunnel, as is shown in Plate V. fig. 3.

3. The Collection of Sirex Parasites for Shipment to New Zealand.

The first attempt at large-scale collection of the parasites was carried out in North Devon during the season 1928–29, the writer having studied the *Sirex* conditions in that area during the previous year. During the summer of 1928 forty breeding-places were prepared consisting of *Sirex* infested logs, about 30 tons of this material being used. The logs were so arranged that the parasites could readily gain access to all parts of the surface and so parasitize the *Sirex* larvae. These logs were left in the woods until the autumn and were then hauled to a central depot, where they were crosscut into short lengths and dissected to obtain the parasite larvae. This method proved successful, 1,753 *Rhyssa* larvae and 113 *Ibalia* larvae having been collected from this material. During the examination of the logs much useful information was obtained, not only with reference to the life-cycle of *Sirex* and its parasites, and their inter-relations, but also as to the most productive type of logs. This information proved extremely valuable during the season 1930–31 when collections were carried out on a much larger scale.

During the autumn of 1930 a survey was made with the object of locating suitable collecting areas. A large area of blown spruce in Montgomeryshire was visited and the presence of numerous *Rhyssa* ovipositors observed sticking in the bark of these trees indicated that this parasite had been actively engaged in oviposition during the summer. Two other estates, one in Bedfordshire and one in Wiltshire, were found to be suitable localities for the collection of parasites, not because *Sirex* was abnormally abundant, but simply on account of the extensive areas of mixed woodlands of the type usually found on large private estates. On both these estates individual coniferous trees, some of which were over-mature or had been damaged by wind, lightning or fungi, were found to support communities of *Sirex*, and each infested tree acted as a focus for the parasites.

During this season's work 6,458 *Rhyssa* larvae and 572 *Ibalia* larvae were collected from the three areas, bringing the total collections to 8,211 *Rhyssa* and 685 *Ibalia*. Of these 7,830 *Rhyssa* and 382 *Ibalia* were shipped to New Zealand.

The collection of this large number of specimens of what had hitherto been regarded as very rare insects was a laborious task; several hundred *Sirex*-infested trees were felled and crosscut into short lengths, each length of timber was then carefully split into small pieces and examined in detail. Over a hundred tons of *Sirex*-infested timber was dealt with in this way, and in order to avoid transportation of the timber to the Laboratory, the greater part of the material was cut up and examined in the forest.

4. The Inter-Relationship of Sirex and the Parasites.

The detailed examination of such a large amount of material provided unique opportunity for the study of the inter-relationship of *Sirex* and its parasites. The data collected explained much that could not previously be understood; they also provided much new knowledge about the biological control of *Sirex*.

During the early stages of the investigation each log or tree examined seemed to produce an entirely different set of conditions, and there appeared to be little hope of correlating the data, but as the work proceeded it became evident that the apparently contradictory data were rapidly being supplemented and gaps being filled.

Before the completion of the work it was possible to construct a complete picture of the *Sirex* biological complex. The knowledge gained was extremely useful in selecting material during the later stages of the work and will greatly simplify the work in future should further supplies of *Sirex* parasites be required.

Standing trees were found to yield the best results. Logs lying on the ground seldom contained more than one generation of *Sirex*, as the bark often becomes loose and they are then unattractive. Once the *Sirex* larvae have become established in a log, they are generally able to complete their development before the timber becomes too decayed.

Sirex-infested logs remain attractive to *Rhyssa* as long as they contain any *Sirex* larvae or pupae, although the log may have ceased to be attractive for *Sirex* oviposition.

The sequence of events in a log infested by *Sirex* is as follows :—The eggs of *Sirex* may be laid at any time from June throughout the summer. The *Sirex* eggs or first-stage larvae may be parasitized by *Ibalia* during the summer provided that the attack by the parasite is made before the *Sirex* larvae have begun to burrow tunnels in the timber, but as *Ibalia* does not normally appear until towards the end of July or later, it is possible for the very early batches of *Sirex* larvae to escape parasitism by *Ibalia*. If the *Sirex* larvae escape parasitism by *Ibalia* at this stage, they are immune from the attack of the parasite throughout the rest of their development, as *Ibalia* is unable to bore holes through the timber with its ovipositor. The eggs of *Sirex* are quite useless to *Rhyssa*, and the *Sirex* larvae during the early stages are equally useless, and although *Sirex* larvae may be attacked by *Rhyssa* at any time during the first summer, they are too small during that period to form suitable hosts, and both the *Sirex* larva and the parasite larva perish.

During the whole of the second summer the *Sirex* larvae are liable to be parasitized by *Rhyssa*. The *Sirex* larvae which were parasitized by *Ibalia* in the first summer lie nearest to the surface and therefore run the greatest risk, as they can be reached by small *Rhyssa* females, while unparasitized *Sirex* often can only be reached by large specimens of *Rhyssa*. Plate III, figs. 1 and 3, show the depth to which *Rhyssa* may reach with her ovipositor. *Sirex* larvae which have been parasitized by *Rhyssa* cease to burrow and are devoured by the parasite larvae. The latter are unable to burrow in the wood and remain in the same spot until ready to emerge as adults in the following summer. The adult *Rhyssa* emerges from the log during the third summer and the exit hole may be found in the log. During the third summer the *Sirex* larvae which escaped *Rhyssa* during the second summer may be parasitized unless they have burrowed too deep into the timber, as sometimes happens in large logs.

In the case of *Sirex* larvae which were originally parasitized by *Ibalia*, the parasite larvae emerge during this period and devour the remains of the host larvae, leaving only the empty skin. The *Ibalia* larvae then rapidly complete their development and remain in the *Sirex* tunnel until the fourth summer, when they pupate, and the adults emerge from the log, as also do the unparasitized *Sirex*, both species having completed their three year life-cycle. The second generation of *Rhyssa* also pupate and emerge. It will be seen, therefore, that during the fourth summer the *Sirex*, *Ibalia* and second generation of *Rhyssa* emerge from the log, leaving exit holes. All the *Sirex* do not escape ; during the spring and early summer they are liable to be parasitized by *Rhyssa* either in the full-grown larval stage, the pupal stage, or even the adult stage, thus producing a third generation of *Rhyssa* which emerge from the log during the fifth summer. Plate IV, fig. 1, shows a third generation *Rhyssa* pupa in the *Sirex* pupal chamber. Plate IV, fig. 2, shows an adult *Rhyssa* of the third generation boring its exit hole from the pupal chamber of *Sirex*.

Table I indicates what a log may be expected to contain in either summer or winter over a period of four years when only one generation of *Sirex* is concerned.

By examination of the contents of a log it is now possible to state accurately whether the log is being examined in the first, second, third, or fourth year of *Sirex* infestation.

Very small standing trees or poles seldom support more than one generation of *Sirex*, if they are heavily infested during the first year. If the diameter of the pole is less than 3 inches the percentage of parasitism may be very high, owing to the fact that the *Sirex* larvae are unable to get out of reach of *Rhyssa* at any stage. These small poles were generally found to be very productive. The small section of timber seen standing on the large log in the top right-hand corner of Plate V, fig. 2, contains exit holes of 14 *Rhyssa* and only one *Sirex*. This section was only 3 inches in length by 2½ inches in diameter and was cut from the base of a small, standing silver fir pole within 6 inches of the ground.

TABLE 1.

Period	*Sirex*	*Ibalia*	*Rhyssa*
1st Summer ...	Oviposits.	Parasitizes some of the *Sirex* eggs.	—
1st Winter ...	Larvae begin to burrow.	Internal parasite.	—
2nd Summer	Larvae about one-third grown.	Internal parasite.	Parasitizes *Sirex* larvae, some of which may contain *Ibalia* larvae.
2nd Winter ...	Larvae about half-grown burrowing towards pith (Plate I, fig. 1).	Larvae feeding as internal parasites.	Larva full-fed lying in gallery of *Sirex*; Plate III, fig. 1, shows two *Rhyssa* larvae which have fed on unparasitized *Sirex* larvae and one *Rhyssa* larva which has fed on a *Sirex* larva previously parasitized by *Ibalia*.
3rd Summer	Larvae about two-thirds grown.	Larvae emerge from *Sirex* host in the spring and destroy remains of the host.	1st generation of *Rhyssa* pupate and emerge from log. *Rhyssa* parasitizes *Sirex* and *Ibalia* larvae giving rise to the 2nd generation of *Rhyssa*.
3rd Winter ...	Larvae are nearly full-grown and are burrowing towards the surface (Plate I, fig. 2).	Larvae full-grown lying in *Sirex* galleries. Plate III, fig. 2, shows two unparasitized *Ibalia* larvae and a *Rhyssa* larva which has fed on *Ibalia*.	Larvae, 2nd generation are full-fed (Plate III, fig. 3).
4th Summer	Pupate and emerge.	Pupate and emerge.	2nd generation pupate and emerge. *Rhyssa* parasitizes *Sirex* pupae and *Ibalia* pupae.
4th Winter ...	—	—	*Rhyssa* larvae 3rd generation with remains of *Sirex* pupa. *Rhyssa* larvae with remains of *Sirex* adult.
5th Summer	—	—	*Rhyssa* 3rd generation emerge (Plate IV, figs. 1, 2).

Very large trees show a wide range in the conditions governing the degree of parasitism. In the thick part of the stem the percentage of parasitism is often very low, owing to the fact that the *Sirex* larvae are out of reach of *Rhyssa* during the second summer and remain out of reach until the spring of the year in which the adults are due to emerge. A few pupae and full-grown larvae are then parasitized (Plate IV, fig. 1), but in large logs many of the pupal chambers are too far from the surface to be reached by the ovipositor of the parasite (Plate II, fig. 2), although the adult *Sirex* are often parasitized as they approach the surface.

The small section in the left-hand top corner (Plate V, fig. 2), is from a large silver fir, the surface of which measures only 5 inches by 2½ inches and contains the exit holes of 8 large *Sirex* and only 1 *Rhyssa*. On the other hand, the upper portions of these large trees show a very high percentage of parasitism. An 8 ft. length, 4 inches in diameter at the thick end and 2 inches in diameter at the thin end, broken from the top of a large silver fir in Devon, yielded 91 *Rhyssa* larvae and only 15 *Sirex* larvae. A small piece 6 inches in length and only 1½ inches in diameter which broke off the tip of the same piece contained 7 *Rhyssa* larvae and no *Sirex*, making a total of 98 *Rhyssa* and 15 *Sirex* in a piece of timber 8 ft. 6 ins. in length and less than 3 inches average diameter. Another similar piece gave 65 *Rhyssa* larvae and 23 *Sirex* larvae.

In the Bedfordshire area a small piece which had been broken from the top of a large silver fir contained 125 *Rhyssa* larvae. In this case every *Sirex* larva had been parasitized. This piece was only 6 ft. in length, was less than 4 inches in diameter at the thick end and tapered to 1½ inches at the thin end. A small silver fir on the same estate 30 ft. in length by about 4 inches average diameter was found to have been entirely missed by *Rhyssa* but was heavily parasitized by *Ibalia*. This tree contained 95 *Ibalia* larvae and 25 *Sirex* larvae, but only one generation of *Sirex*, and reference to the tables showing the rate of development clearly indicates that the log was examined at a stage corresponding with the third year of infestation. Both the *Sirex* and *Ibalia* adults would normally have emerged from the log during the following summer. This was the only tree found in any of the four areas which showed a high percentage of parasitism by *Ibalia*, but this is doubtless because it was the only tree examined in which no *Rhyssa* larvae were found. Many examples afforded strong evidence that *Ibalia* is normally heavily super-parasitized by *Rhyssa*. It seems probable that some of the remaining *Sirex* and a large proportion of the *Ibalia* would have been parasitized by *Rhyssa* during the following summer before the adults were ready to emerge.

A silver fir on the Wiltshire estate 55 ft. in length by 6 inches average diameter yielded 459 *Rhyssa* larvae, 29 *Ibalia* larvae and 139 *Sirex* larvae. In this case two generations of *Sirex* larvae were present, and it is unfortunate that the *Sirex* larvae were not dissected as it is almost certain that a number of them would have been found to contain *Ibalia* larvae, and a more accurate and higher percentage of parasitism would have been obtained. In this case also, the population was liable to be further attacked by *Rhyssa* during the following summer. It will be seen, therefore, that the actual percentage of parasitism would have been much higher than the above figures indicate.

These five cases cannot be regarded as typical examples. They represent the highest percentages of parasitism found in several hundred trees examined.

TABLE II.

Locality	Host tree	*Sirex*	*Rhyssa*	*Ibalia*
Devon ...	Silver fir	15	98	—
Devon ...	Silver fir	23	65	—
Bedford ...	Silver fir	—	125	—
Bedford ...	Silver fir	25	—	95
Wilts	Silver fir	139	459	29
	Totals	202	747= 69·61 per cent.	124= 11·55 per cent.

The five cases taken together show that of a total of 1,073 *Sirex* larvae 871 (81 per cent.) had been parasitized. The figures cannot be regarded as final, however, since the remaining 202 *Sirex* larvae were still liable to be parasitized by *Rhyssa* during the early part of the following summer before they emerged as adults, and the exceptionally large number of *Rhyssa* adults which would emerge from this small amount of material increases the probability that a large proportion of the *Sirex* larvae would be parasitized. These figures serve to show that under conditions which are favourable to *Rhyssa* the percentage of parasitism may be very high. Where the conditions are unfavourable, owing to the diameter of the log in which *Sirex* may be breeding, the percentage of parasitism may be very low. Nevertheless, no cases were found where colonies of *Sirex* had entirely escaped attack by both parasites.

The following is a summary of the number of each species obtained from the various localities :—

TABLE III.

Season	Locality	*Rhyssa*	*Ibalia*
1928–29 ...	North Devon ...	1,753	113= 6·05 per cent.
1930–31 ...	Montgomeryshire ...	3,792	210= 5·53 ,, ,,
1930–31 ...	Bedfordshire ...	713	247=34·64 ,, ,,
1930–31 ...	Wiltshire	1,953	115= 5·88 ,, ,,
	Totals ...	8,211	685= 7·70 per cent.

These figures show a close resemblance in the proportion of *Rhyssa* and *Ibalia* found in the Devon, Montgomeryshire and Wiltshire areas, as compared with the Bedfordshire area, but as the 95 *Ibalia* found in one small tree represent approximately two-fifths of the total collected in the whole area, this largely accounts for the difference.

The above figures do not represent the true ratio of the *Rhyssa* and *Ibalia* population, because while all the *Rhyssa* larvae were collected, only full-grown *Ibalia* larvae were collected. It must be remembered that the *Ibalia* larvae are internal parasites during the early stages and many of the *Sirex* larvae under two years of age contained *Ibalia* larvae, but at the time it was considered that these larvae would be useless for shipment, and they were thrown away and are not therefore included in the number of *Ibalia* larvae collected. At a later date the writer collected some of these parasitized *Sirex* larvae and kept them in tubes. The *Sirex* larvae continued to live until the *Ibalia* emerged. These *Ibalia* subsequently completed their development. From this it would appear that the best time to collect *Ibalia* larvae for shipment would be during the early stages while they are inside the *Sirex* larvae.

Logs cut from large standing trees were frequently found to contain three generations of *Sirex* and a period of seven years elapses between the time when the first *Sirex* eggs are laid to the time when the last of the parasites emerge from the timber. Trees of this description gave rise to three generations of *Sirex*, three generations of *Ibalia* and five generations of *Rhyssa*. The contents of such a tree varies from year to year and an entirely different combination of insects in various stages of development is to be found according to the year in which the material is examined. Each of these large trees represents a separate *Sirex* colony and the composition of the population is often very complex owing to the different stages in which the various species are to be found at any given time. This rendered the task

TABLE IV.

Inter-relations of Sirex, Ibalia *and* Rhyssa *in a tree in which three successive generations of* Sirex *breed.*

Period	*Sirex*	*Ibalia*	*Rhyssa*
1st Summer ...	Oviposits 1st gen.	Parasitizes eggs or young larvae.	—
1st Winter ...	Larvae begin to burrow.	Eggs or 1st stage larvae inside *Sirex* larvae.	—
2nd Summer	Larvae 1st gen. about one-third grown; oviposits 2nd generation.	Larvae feeding as internal parasites; parasitizes 2nd gen.	Parasitizes *Sirex* larvae of 1st gen., some of which contain *Ibalia*.
2nd Winter ...	Larvae 1st gen. about half grown; larvae 2nd gen. begin to burrow.	Larvae feeding as internal parasites in 1st and 2nd gen. *Sirex*.	Larvae 1st gen. lying full-fed in *Sirex* galleries (Plate III, fig. 1).
3rd Summer	Larvae 1st gen. about two-thirds grown; larvae 2nd gen. about one-third grown; oviposits 3rd gen.	Larvae 1st gen. emerge from host and devour remains; 2nd gen. internal parasites; oviposits 3rd gen.	1st gen. pupate and emerge; oviposits 2nd gen. on larvae of *Sirex* and *Ibalia* of 1st gen. also on larvae of *Sirex* 2nd gen., some of which may contain *Ibalia* larvae.
3rd Winter ...	Larvae 1st gen. full-grown (Plate I, fig. 2); larvae 2nd gen. about half grown (Plate I, fig. 1); larvae 3rd gen. begin to burrow.	Larvae 1st gen. full-grown lying in pupal chamber (Plate III, fig. 2); larvae 2nd and 3rd gen. internal parasites.	Log contains exit holes of 1st gen.; larvae of 2nd gen. which have fed on 1st gen. *Sirex* and *Ibalia* larvae are full-grown; larvae of 2nd gen. which have fed on 2nd gen. *Sirex* larvae are full-grown.
4th Summer	1st gen. pupate and emerge; 2nd gen. about two-thirds grown; 3rd gen. about one-third grown.	1st gen. pupate and emerge; 2nd gen. emerge from host larvae; 3rd gen. internal parasites.	2nd gen. pupate and emerge. Oviposits 3rd gen. on *Sirex* and *Ibalia* pupae of 1st gen., also on *Sirex* and *Ibalia* larvae of 2nd gen. and *Sirex* larvae of 3rd gen.
4th Winter ...	Log contains exit holes of 1st gen.; larvae 2nd gen. full-grown; 3rd gen. about half grown.	Log contains exit holes of 1st gen.; larvae 2nd gen. lying full-grown; larvae 3rd gen. internal parasites.	Log contains exit holes of 1st and 2nd gens.; larvae of 3rd gen. full-grown (Plate V, fig. 3).
5th Summer	2nd gen. pupate and emerge; 3rd gen. about two-thirds grown.	2nd gen. pupate and emerge; 3rd gen. emerge from host larvae.	3rd gen. pupate and emerge; 4th gen. oviposits on pupae of *Sirex* and *Ibalia* 2nd gen. and larvae of *Sirex* and *Ibalia* 3rd gen.
5th Winter ...	Log contains exit holes of 1st and 2nd gens.; larvae 3rd gen. full-grown.	Log contains exit holes of 1st and 2nd gens.; larvae 3rd gen. full-grown.	Log contains exit holes of *Sirex* 1st, 2nd and 3rd gens.; larvae 4th gen. full-grown.
6th Summer	3rd gen. pupate and emerge.	3rd gen. pupate and emerge.	4th gen. pupate and emerge; oviposits 5th gen. on pupae of *Sirex* and *Ibalia* of 3rd gen.
6th Winter ...	Log contains exit holes of 1st, 2nd and 3rd gens.	Log contains exit holes of 1st, 2nd and 3rd gens.	Log contains exit holes of 1st, 2nd, 3rd and 4th gens.; larvae fed on *Sirex* and *Ibalia* pupae full-grown.
7th Summer	—	—	5th gen. pupate and emerge.

of the solution of the general problem more difficult, but the examination of the contents of large numbers of trees and the careful comparison of contents of each tree with the types of exit holes found in the bark, enabled the writer to work out the inter-relationships of the species concerned.

Table IV shows what a tree of this description may be expected to contain at any period during the development of the colony.

With a view to ascertaining the approximate number of *Sirex* and parasites such a tree would produce, a silver fir showing *Sirex* holes of last summer and the previous summer was selected for examination. This tree was 50 ft. in length by 8½ inches qqt. under bark. A section 6 ft. in length from the middle of the tree showed 376 exit holes and contained 31 *Sirex* larvae of the 3rd generation ready to pupate, and 11 *Rhyssa* larvae. The exit holes were fairly evenly distributed over the whole surface of the tree, so that taking this 6 ft. section as a basis, it will be seen that a tree of 25 c. ft. had supported more than 3,000 *Sirex* and parasites. A 3 ft. section of this tree is seen on Plate V, fig. 2. It was, of course, quite impossible to undertake the task of determining the percentage of parasitism, as this would necessitate an examination of each pupal chamber and exit hole. This is the only way in which it is possible to determine with certainty whether an exit hole is that of *Sirex* or a parasite. Owing to the great variability in size of *Sirex* and *Rhyssa*, the external appearance of the exit hole gives no definite clue, except in the case of very large holes such as will accommodate the end of an ordinary lead pencil. These are obviously made by large female *Sirex*, as seen in Plate II, fig. 2. Holes a little smaller may be those of male *Sirex* or very large *Rhyssa* (Plate IV, fig. 2). Very small holes may be those of *Ibalia* or small *Rhyssa*. More than half the holes in the log were too small to be those of *Sirex*. The exit holes of *Sirex* may readily be distinguished from those of *Rhyssa* or *Ibalia* by examining a longitudinal section of the pupal chamber and exit hole. The pupal chamber of *Sirex* is entirely without lining and the diameter is approximately the same as that of the exit tunnel.

The pupal chamber of *Rhyssa* is lined with a thin cocoon. This can be seen in Plate V, fig. 1, and the diameter of the exit tunnel is considerably less than the diameter of the pupal chamber, which, of course, was made by the full-grown *Sirex* larva.

The exit tunnel of *Ibalia* is less in diameter than the pupal chamber but as there is no lining to the latter it can by this means be distinguished from that of *Rhyssa*.

Although the exit tunnel of *Ibalia* is, on the average, less in diameter than that of *Rhyssa*, it will readily be seen that owing to a large number of *Ibalia* larvae being parasitized by *Rhyssa*, the size of the exit hole cannot be taken as a criterion.

In discussing the inter-relations of *Ibalia* and *Rhyssa* in his paper on "Studies of the *Sirex* parasites" (pp. 55–57), Dr. Chrystal (1930) gives detailed particulars of the contents of a larch log, as reproduced below :—

Sirex, Ibalia *and* Rhyssa *obtained from a larch log (Brandon, Suffolk), 11–20th June, 1929.*

Ibalia			*Sirex*		*Rhyssa*	
Larvae Full-grown	Prepupae	Pupae	Larvae	Pupae	Pupae	Adults
140	5	39	152	68	3	7
Total : 184 = 44·4 per cent.			Total : 220 = 53·1 per cent.		Total : 10 = 2·4 per cent.	

Grand Total : 414.

He states : " The above total, representing, as it does, the total population of a single tree, indicates that the abundance of *Ibalia* in the Brandon area can be correlated with the scarcity of *Rhyssa* in the same region. One further observation of interest was obtained from the Brandon log. The *Sirex* were practically all in the advanced larval or pupal stage ; the *Ibalia* were in the majority of cases about to pass into the pre-pupal state and would have emerged this year, while the *Rhyssa* were also in the pupal or adult stage. Last season had evidently witnessed the emergence of quite a number of wood-wasps and parasites (most of the latter, to judge by the tunnels, were also *Ibalia*) and this season will probably see the last of the wood-wasp-parasite population leave the tree. This uniformity of development was very striking and is comparable to similar cases which have been found in logs from Dorset."

The present writer considers that the above figures and remarks give an inaccurate interpretation of the biological complex which they are intended to explain. In the first place, it is to be noted that Dr. Chrystal regards the whole of the population of the larch tree as forming one generation of *Sirex* and its parasites, and assumes that the whole of this population would normally reach maturity and emerge from the tree during the current season. However, the log contents clearly indicate that two generations of *Sirex*, two generations of *Ibalia* and only part of one generation of *Rhyssa* are present. Dr. Chrystal states that " The *Ibalia* were in the majority of cases about to pass into the pre-pupal state and would have emerged this year," but his own published life-cycle of *Ibalia* (Table C., p. 52) reproduced below, does not agree with this hypothesis.

TABLE C.

Distribution of Stages in a Three Year Life-cycle of Ibalia

Year	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
1927 ...								E	E	E	E 1	E 1
1928 ...	E 1	E 1	E 1	E 1	E 1	E 1	E 1 2	E 1 2	1 2 3	1 2 3	1 2 3	1 2 3
1929 ...	2 3	2 3	2 3	3	3	3 4	3 4	3 4	3 4	4	4	4
1930 ...	4	4	4	4	4	P	P	A	A			

E. = Embryonic stage.
1, 2, 3, 4. = Larval Stages.
P. = Pupa.
A. = Adult.

During several seasons the present writer has bred *Ibalia* from parasitized *Sirex* larvae and in each case the results have corresponded with those of Dr. Chrystal as shown in the above table. Reference to the Table IV, showing the inter-relations of *Sirex* and its parasites, indicates that the contents of the Brandon larch log correspond exactly with what we might expect to find in a log during the 5th summer of infestation, and that it would be as follows :—

TABLE V.

Sirex	*Ibalia*	*Rhyssa*
Pupae of 2nd gen. due to emerge as adults during summer of 1929.	Pupae of 2nd gen. due to emerge as adults during summer of 1929.	Pupae and adults 3rd gen. due emerge during 1929.
Larvae of 3rd gen. two-thirds grown remain in log until summer of 1930.	Larvae of 3rd gen. emerge from host larvae and remain in log until summer of 1930.	—

Dr. Chrystal further assumes that no *Rhyssa* adults have emerged from the log during the current season, notwithstanding the fact that he has already stated on page 55, that *Rhyssa* oviposition was at its height in May and June, during that season. This clearly implies that a very large proportion of the *Rhyssa* adults had emerged during May and June, since there is no evidence that *Rhyssa* ever survives the winter in the adult stage after having emerged from the timber. On 15th April, 1932, the present writer found a number of young *Rhyssa* larvae feeding on *Sirex* larvae in a larch log in Verulam Woods, near St. Albans. This indicates that *Rhyssa* may emerge and commence to oviposit as early as the beginning of April. As already stated, during the whole of the operations mentioned above no larvae of *Rhyssa* were found feeding between the end of November and the end of March. It will be observed that the examination of the Brandon larch log began on 11th June, and was completed on 20th June, 1929. In these circumstances it is not unreasonable to suppose that a large proportion of the *Rhyssa* adults had emerged and were not included in the figures on which the percentage of parasitism has been based. This element of uncertainty makes the figures of little value so far as the relative percentage of parasitism is concerned, but even if the log had been examined at the beginning of May and all the *Rhyssa* of the 3rd generation had been collected, the figures would not have given the correct percentage of parasitism, for several reasons. In the first place the *Sirex* larvae of the 2nd generation had already produced one generation of *Rhyssa* which had emerged during 1928, and the pupae were still liable to be parasitized during the summer of 1929, producing a further generation of *Rhyssa* adults which would emerge in 1930. The 152 *Sirex* larvae of the 3rd generation and the 140 *Ibalia* larvae of the 3rd generation found in the log would be subject to parasitism by *Rhyssa* during the summer of 1929, producing part of the generation of *Rhyssa* which would emerge as adults in 1930. While the *Sirex* and *Ibalia* larvae which escaped parasitism in 1929 would still be liable to parasitism by *Rhyssa* during the summer of 1930 while in the pupal stage, thus giving rise to the last generation of *Rhyssa* which would emerge as adults in 1931. It will be seen, therefore, that the *Rhyssa* found in a log in any one year do not represent the total number produced by a single generation of *Sirex*, since each generation of *Sirex* may, and normally does, produce three generations of *Rhyssa*. On the other hand, the problem is still further complicated by the fact that two or even three generations of *Sirex* may be present in the log at the same time. In this case each of the generations of *Sirex* will be liable to be parasitized and together will give rise to one and the same generation of *Rhyssa*. To illustrate this, let us suppose that the above Brandon larch log had been examined a year earlier. This would have been during the summer of 1928. It would at that stage have corresponded with the 4th summer as shown in Table IV and would have been found to contain :—

TABLE VI.

Sirex	*Ibalia*	*Rhyssa*
1st gen. pupae.	1st gen. pupae.	2nd gen. fed on 1st gen. *Sirex.*
2nd gen. larvae two-thirds grown.	2nd gen. full-grown larvae.	3rd gen. fed on 2nd gen. *Sirex.*
3rd gen. larvae one-third grown.	3rd gen. internal parasites.	

The 1st generation *Sirex*, 1st generation *Ibalia* and 2nd generation *Rhyssa* would emerge from the log during the summer of 1928, leaving the 2nd and 3rd generations of *Sirex* and the 2nd and 3rd generations of *Ibalia* to develop along with the 3rd generation of *Rhyssa* to which they would give rise. During the summer of 1928, the 2nd generation of *Rhyssa* would have six possible types of hosts, consisting of the pupae of *Sirex* 1st generation, pupae of *Ibalia* 1st generation, larvae of *Sirex* 2nd generation which had escaped being parasitized by *Ibalia*, full-grown larvae of *Ibalia* of the 2nd generation from *Sirex* 2nd generation, *Sirex* larvae of the 3rd generation which contained *Ibalia* larvae of the 3rd generation as internal parasites, and unparasitized larvae of *Sirex* of the 3rd generation. These six types of host may, for convenience, be regarded as three groups, since the 1st generation of *Ibalia* corresponds with the 1st generation of *Sirex*, while the second generation of *Ibalia* corresponds with the 2nd generation of *Sirex*, and the 3rd generation of *Ibalia* corresponds with the 3rd generation of *Sirex*. It only remains to be remembered that the *Ibalia* larvae of the 3rd generation are internal parasites in the one-year-old 3rd generation *Sirex*, that the *Ibalia* larvae of the 2nd generation emerge from the host larvae in the spring and lie full-grown in the *Sirex* galleries, while the corresponding 2nd generation *Sirex* larvae are about two-thirds grown, and that the 1st generation of *Sirex* and *Ibalia* are both in the 3rd year of their development and are therefore in the pupal stage during the early part of the summer and emerge as adults later in the season.

The following diagram indicates from which generation of hosts each generation of *Rhyssa* arises, and also shows how each generation of *Sirex* may produce three generations of *Rhyssa*.

TABLE VII.

Period	*Sirex*	*Rhyssa*
1st Summer, 1925	Eggs, 1st gen.	—
2nd Summer, 1926	1st gen., 1 year old, one-third grown Eggs, 2nd gen.	—
3rd Summer, 1927	1st gen., 2 years old, two-thirds grown 2nd gen., 1 year old, one-third grown Eggs, 3rd gen.	1st generation.
4th Summer, 1928	1st gen., 3 years old pupate and emerge 2nd gen., 2 years old, two-thirds grown 3rd gen., 1 year old, one-third grown	2nd generation.
5th Summer, 1929	2nd gen., 3 years old pupate and emerge 3rd generation, 2 years old, two-thirds grown	3rd generation.
6th Summer, 1930	3rd gen., 3 years old pupate and emerge	4th generation.
7th Summer, 1931		5th generation.

It will be seen that the 1st generation of *Sirex* produces the 1st generation of *Rhyssa* and also contributes to the 2nd and 3rd generations. The 2nd generation of *Sirex* contributes to the 2nd, 3rd and 4th generations of *Rhyssa*, while the 3rd *Sirex* generation contributes to the 3rd and 4th generations and produces the 5th generation.

The above is intended to illustrate what normally takes place in a single tree in which three successive generations of *Sirex* are bred. It must not be supposed that the 1st generation of *Rhyssa* necessarily gives rise to the 2nd generation and the 2nd to the 3rd, and so on. Actually, in the forest all sorts of combinations are found to occur. Some logs contain only one generation of *Sirex*, others two or even three generations. *Rhyssa* adults of the 1st generation from one log may give rise to the 1st, 2nd, 3rd, 4th or 5th generation in another log, while *Rhyssa* adults of the 5th or any other generation may do the same, but this does not in any way alter the sequence of events.

Let us further examine the Brandon larch tree. As we have seen, the 1st generation of *Rhyssa* emerged in 1927. The 1st generation *Sirex*, 1st generation *Ibalia* and 2nd generation *Rhyssa*, emerged during the summer of 1928. In June 1929 the tree contained the 2nd generation of *Sirex*, and the 2nd generation *Ibalia*, both in the pupal stage and due to emerge during that season. It also contained the 3rd generation *Sirex* and the 3rd generation *Ibalia*. These would remain in the larval stage until the summer of 1930, when they would normally pupate and emerge as adults. In addition it contained pupae and adults of the 3rd generation of *Rhyssa* ; an indefinite number of this generation of *Rhyssa* had emerged during the months of May and June. These *Rhyssa* had been parasitic on the *Sirex* and *Ibalia* of the 2nd and 3rd generations. A proportion of the *Rhyssa* of the 2nd generation which emerged in 1928 had also been parasitic on the 2nd generation of *Sirex* during the season 1927–28, at which time the 2nd generation of *Ibalia* larvae would be internal parasites. It will be seen that, in order to arrive at the correct percentage of parasitism, it would be necessary to include these two numbers in the calculation. This would give a considerably higher percentage of *Rhyssa* and a lower percentage of *Ibalia* and unparasitized *Sirex*. The effect of the 4th and 5th generations of *Rhyssa* would be to increase still further the percentage of *Rhyssa* and lower the percentage of *Ibalia* and unparasitized *Sirex*.

The above analysis shows the futility of trying to arrive at an accurate estimate of the percentage of parasitism by *Rhyssa* by means of calculations based on the contents of a single log or on a single generation. In fact, it is very difficult, if not quite impossible, to arrive at an absolutely accurate estimate of the percentage of parasitism. In the case of *Rhyssa* the difficulty is due to the fact that one generation of the host may produce three generations of the parasites over a period of three years, and, as we have seen, when three generations of hosts are present in the log the second generation of *Rhyssa* is produced by two generations of hosts, the 3rd generation of *Rhyssa* is produced by three generations of hosts and the 4th generation of *Rhyssa* is produced by two generations of hosts ; while figures obtained by calculations based entirely on the young *Sirex* larval stages cannot be considered final, because the percentage is liable to be modified by one or even two subsequent generations of *Rhyssa*.

In the absence of *Rhyssa* it would be fairly easy to ascertain the percentage of parasitism by *Ibalia*, as in this case all that would be necessary would be to collect and dissect all the *Sirex* larvae found in the logs during the winter months, adding to the numbers of parasitized larvae the total number of full-grown *Ibalia* larvae found in the material. The addition of the number of full-grown *Ibalia* larvae is essential, because results based entirely on dissected *Sirex* larvae would show a percentage of parasitism below the actual figure, unless all the material examined happened to be in the early stages, *i.e.*, during the first or second winter of infestation. In this case only one generation of host and parasite would be present and no full-grown

Ibalia larvae would be found. Logs collected from localities where an infestation has been in progress for more than two years would almost certainly include some material over two years of age, in which case full-grown *Ibalia* larvae would be present. It is imperative that only material collected from logs during the winter and early spring be included in the figures, as material collected from June to October, inclusive, would vitiate the results, owing to the fact that the population is in a state of flux during the summer and autumn and there is no certainty that the contents of logs examined during that period will represent the actual population. Where *Rhyssa* is present the true percentage of parasitism by *Ibalia* cannot be ascertained by the dissection of *Sirex* larvae collected from a number of logs selected at random, as *Rhyssa* is intrinsically superior to *Ibalia*, and the effects of parasitism by *Rhyssa* are cumulative during each generation of *Sirex*.

In any case it would be necessary to ascertain how many adults of each species had already emerged from the logs in order to ascertain the percentage of parasitism by either species where the infestation has been in progress for more than two years. Unfortunately Dr. Chrystal's figures, given in Appendix II of his paper, showing the percentage of parasitism by *Ibalia*, are based entirely on the results of the dissection of *Sirex* larvae collected from logs selected at random during all seasons of the year.

5. Possible Factors of Control, other than Parasites.

The writer has paid considerable attention to the study of factors, other than parasites, which might be expected to operate in the control of *Sirex* wood-wasps. The results of his observations in this direction, although almost entirely negative, are given below.

(*a*) *Birds*.

It is reasonable to expect that birds would play an important part in the control of a forest insect which spends a considerable part of its time boring oviposition holes in the bark of standing trees and felled logs, but the writer failed to observe a single instance of either *Sirex* or *Rhyssa* adults being attacked by birds.

Robins, wrens and titmice were observed to extract *Sirex* larvae from the ends of logs which had been crosscut, but none of these birds appeared to take the slightest notice of *Sirex* and *Rhyssa* adults which were ovipositing within 2 or 3 ft. of them. On one occasion a spotted flycatcher was seen to use a stack of *Sirex*-infested logs as a jumping-off place for its characteristic short flights to capture insects, but it made no attempt to catch the *Sirex* and *Rhyssa* adults which were ovipositing in the logs, or flying around the stack of logs in considerable numbers.

Sirex gigas certainly bears some resemblance to a wasp or hornet, and when touched while on the surface of a log *Sirex cyaneus* erects the abdomen in much the same way as the Devil's coach-horse beetle, to which insect it bears some resemblance in colour. The bright metallic lustre and somewhat piebald appearance of *Rhyssa* may suggest that the insect is inedible. Whether either the colour or habits of these insects afford them some measure of protection from birds is a matter for conjecture.

Of the hundreds of *Sirex*-infested trees cut up during the collection of parasite larvae, not a single silver fir tree showed any sign of the attack of woodpeckers. Other trees which were in a somewhat advanced stage of decay were favourite feeding-places for woodpeckers, but on examination these trees were found to contain *Rhagium* larvae, pupae and adults, and although many of them were perforated with numerous *Sirex* and *Rhyssa* exit holes, these trees were obviously too decayed for further use by *Sirex*, and no *Sirex* larvae were found in them.

Woodpeckers were frequently observed enlarging *Sirex* exit holes in trees and on examination similar exit holes were found to contain woodlice, hibernating flies and in some cases hibernating Chalcids. Birds are frequently observed at work on larch trees from which *Tetropium gabrieli* adults have emerged, and the exit holes of this insect seem to be a favourite hunting place.

Both *Tetropium* and *Sirex* attack the bark of sickly larch as soon as the tree is in a suitable condition for their breeding purposes. *Tetropium* completes its life-cycle in one year and although this species may not attack the tree until the year following the attack of *Sirex*, the *Tetropium* adults will have emerged while *Sirex* is still in the larval stage. This has led to the belief, expressed by some writers on forest entomology, that *Sirex* is secondary to *Tetropium* in its attack on the tree, which is certainly not the present writer's experience.

It has already been mentioned that the larval tunnels and pupal chambers of *Sirex* are often of a very superficial character in larch timber. This is particularly the case when the *Sirex* larva has been parasitized by *Ibalia*. In the majority of cases the larvae of *Ibalia* lie within a quarter of an inch of the surface of the timber and are often lying in that position during the period when the grestest activity of birds on the bark of larch takes place, namely during the winter following the summer during which *Tetropium* adults have emerged from the bark. In these circumstances it is not unreasonable to suppose that the *Ibalia* larvae may often be extracted and eaten by the birds.

The pupal chambers of the male *Sirex* often occupy this superficial position, so they also are particularly liable to destruction by birds. The pupal chamber of female *Sirex* are generally formed at a greater distance from the surface, but as seen in Plate V, fig. 3, they sometimes lie quite close to the surface, and as in all cases the larvae or pupae which occupy this superficial position in the timber are exceptionally liable to parasitism by *Rhyssa*, it will be seen that birds probably destroy more *Ibalia* and *Rhyssa* larvae than *Sirex* larvae.

During the collection of parasite larvae, *Tetropium*-infested larch trees which had been heavily attacked by birds were found to contain few *Sirex* parasites, consequently preference was given to silver fir, spruce, pine, and larch trees which did not show much sign of bird activities. The fact that an insect does not appear to be attacked by birds, or at any rate is not particularly attractive to them, during periods when the insect is comparatively scarce as compared with other species of insects on which the birds are observed to be feeding, must not be taken as evidence that the insects will be ignored, or even remain unattractive, during periods when other insects are not particularly numerous, or in localities or environments where other insects are relatively scarce, or when that particular species is exceptionally numerous, as in the case of an outbreak.

It is well known that birds often congregate in large numbers when an outbreak of the Oak Leaf-roller moth occurs, to devour these insects. In such circumstances birds which are not normally insectivorous are to be found feeding on insects ; in the case of the Large Larch Sawfly infestation during the year 1906-1912, Hewitt (1912) states that starlings, jackdaws and rooks fed on the larvae in company with other birds, and Annand (1910) records that jays were very useful in extracting the sawfly larvae from the cocoons.

Although the present writer (1937) in discussing birds in relation to bark-beetle control, states that birds cannot be regarded as important factors in the control of bark-beetles under normal conditions in Britain, this is certainly not the case where large bark-beetle infestations arise, as sometimes happens in Europe. Trägårdh and Butovitsch (1938) state that in Sweden during an extensive bark-beetle infestation, birds destroyed immense numbers of the insects during the swarming period.

In the case of *Sirex*, Clark (1927) states that in New Zealand birds destroy considerable numbers of the insects. Their beneficial effects will, however, be greatly nullified if they also destroy the parasites, which have been introduced and liberated to control the wood-wasps.

(*b*). *Fungi.*

No evidence has been found to show that entomophagous fungi play any part in the control of *Sirex*, but certain species of phytophagous fungi cause the death of coniferous trees and are of considerable importance as agents contributing to the provision of suitable breeding material. Under certain conditions, however, these same fungi cause the death of *Sirex* pupae and adult insects.

During the winter of 1928–29 the writer personally cut up and dissected upwards of 30 tons of timber which had been used for the purpose of forming breeding-places for the parasites of *Sirex* during the previous summer. The bulk of this timber consisted of silver fir from the plantations in North Devon referred to later. Some of the trees had been killed by *Fomes annosus* (Fr.) Cooke = *Tranmetes radiciperda*, Hartig, and others by *Armillaria mellea*, Vahl. = *Agaricus melleus*, L. The methods of attack and the effects of the two fungi are quite different, trees severely attacked by the latter generally die quickly, often within one or two years, while large trees attacked by the former may live for a considerable number of years. In the case of *Fomes annosus* the fungus attacks and kills the roots and the mycelium of the fungus attacks the heartwood, causing the tree to become hollow for several feet at the base of the stem. Large trees which have only a few of the roots attacked may continue to flourish and put on wide annual rings of timber, although the fungus may be actively destroying the heartwood, but if many of the roots are killed the trees are liable to be blown or may die standing. In either case the timber not actually invaded by the mycelium of the fungus is sound and indistinguishable from that of trees which have not been attacked. Once the vigour of the tree is reduced to the point when the foliage begins to wilt, whether standing or blown, the timber is attacked by *Sirex*, but in no case were the *Sirex* larvae found burrowing into timber which had become permeated by the mycelium of this fungus.

Armillaria mellea attacks the tree roots and the base of the stem just below ground-level. The mycelium of the fungus invades the cambium layer and spreads rapidly upwards between the bark and the timber. When once the base of the stem has been completely encircled by the mycelium of the fungus, the foliage wilts and the whole tree at once becomes suitable for the attack of *Sirex*. This type of tree is undoubtedly one of the most attractive breeding-places.

When the mycelium of the fungus reaches the stranded rhizomorph stage between the bark and the timber, the bark becomes loose and that portion ceases to be attractive for oviposition. At this stage the sapwood has become permeated by the fungus. In the meantime the *Sirex* larvae which hatched from the eggs of the previous season have begun to burrow towards the heartwood, which is still quite sound. Here they continue to feed until the autumn preceding the summer when they are due to emerge as adults. They then turn outwards and burrow through the sapwood, which may by this time have become quite decayed. In no instance were *Sirex* larvae found feeding in this fungus-infested material, and even the fully developed larvae do not in all cases successfully pupate and emerge as adults. Some of the pupae are destroyed by the fungus, and adults not infrequently perish. It is to this material that Dr. Chrystal refers in " *Sirex* Wood-wasps and their Importance in Forestry " (p. 235) when he states " The pupae of *S. cyaneus* when lying too deep in the wood often perish in situ, either in the pupal stage or as adults. For example, while examining silver fir logs for *S. gigas* material recently, I was struck by the number of adults that were found dead in their tunnels, sometimes in the pupal chamber, sometimes on their way to the outside. These adults were nearly always covered with fungus, but whether this fungus was the cause of death or an after-growth I do not know ; but I imagine that the death of the pupae and likewise that of the adults is due to some organism whose attack is induced by change of moisture conditions in the wood."

The particular logs to which he refers had been lying for some time on the ground, and the conditions had, therefore, been favourable for the rapid development of the fungus. While the trees remain standing the fungus develops more slowly and fewer deaths occur.

Buchner (1928) described special organs in *Sirex* and *Xyphydria* that harbour a fungus and provide for its transmission to the offspring, and regards this as a case of symbiosis. This has given rise to much speculation during recent years. Professor J. W. Munro (1931) suggested that the fungus acts as a pre-digestive and that *Sirex* larvae can develop only in material that is in a condition suitable for the development of the fungus, which has been identified as a species of *Stereum*.

On the other hand, Mansour and Mansour-Bek (1934) have shown that the true wood-feeding insects do not depend on micro-organisms for the digestion of wood. They comprise those without cellulose-breaking enzymes, which derive the necessary carbohydrates from the soluble sugar and starch in the wood on which they feed, and those with such enzymes, which can utilise the cellulose of the wood through the activity of their own secretions, and can therefore live on wood relatively poor in the simpler carbohydrates.

As a biological study symbiosis is a subject of great interest, but for all practical purposes, so far as the control of *Sirex* is concerned, the symbiont may be regarded as the equivalent of part of the insect.

(*c*). *Climatic and Physical Conditions.*

The range in extremes of climatic conditions in Britain is not sufficiently great to have any apparent effect on the development of *Sirex*. Both *Sirex gigas* and *S. cyaneus* are present at all elevations or latitudes suitable for the growth of the host trees. In the neighbourhood of the Cairngorms in Scotland, temperatures of —5°F. are frequently registered in winter, but *Sirex* does not appear to be adversely affected by these severe conditions. The writer has often examined the contents of logs during periods of severe frost and has found both *Sirex* and *Rhyssa* larvae completely encased in a layer of ice within the pupal chamber, but on being thawed out the larvae did not manifest any signs of having suffered ill effects, and other larvae in the same logs subsequently completed their development.

A period of severe drought sometimes has the effect of causing logs to dry out and become unattractive for *Sirex* oviposition, and in the case of logs which are already infested by *Sirex*, the development of the larvae may be arrested somewhat, and adult *Sirex* which have developed in exceptionally dry logs are often very small.

On the other hand, periods of severe drought often benefit the *Sirex* population as a whole by causing a serious reduction of the water level in the subsoil resulting in the death, or partial destruction, of overmature trees, which then become available for breeding purposes, so that on the whole, the conditions produced by drought are perhaps more favourable for *Sirex* increase than otherwise.

During prolonged wet periods the sapwood of logs, which have been lying in the forest for several seasons, becomes thoroughly saturated with water, and in the case of logs lying in wet places many of the *Sirex* larvae and pupae are killed by excess of moisture. But as the parasite larvae suffer in the same way the ratio of host and parasite will not be altered, and the only effect will be a slight reduction in the general population.

Here again, the conditions which, on the one hand, cause destruction to part of the insect population, compensate by the addition of benefits which these same conditions produce for the population as a whole. Prolonged wet periods cause low-lying land to become water-logged, often resulting in an unhealthy condition, or even the death of groups of trees which are unable to withstand exceptionally wet conditions. These trees are thus rendered suitable for the breeding purposes of *Sirex*.

Gales and snowbreak also provide large quantities of suitable breeding material. In fact it seems probable that all abnormal conditions in the forest ultimately result in more favourable breeding facilities, and consequently the increase of the *Sirex* population, and that with the exception of parasites, *Sirex* has no known natural enemies of any importance.

6. The Economic Status of Sirex in Britain.

The attack of *Sirex* on the tree is entirely for breeding purposes, and its activities in this respect are confined to the timber. The nature of the damage is of a technical character affecting the quality of the timber.

In common with other insects which breed in the bark or timber of standing trees, *Sirex* will attack any part of the tree as soon as that part is in a condition suitable for its requirements. In a spruce wood near Dulverton, Somerset, the writer saw exit holes of *Sirex* in a large bare patch of timber on the side of a big spruce tree from which the bark had been worn by the friction caused by a wire rope during haulage operations. Owing to the extent of the damage to the bark, occlusion had not been complete, although the rest of the tree was in a very flourishing condition.

Sirex sometimes makes mistakes and attacks trees which are not in a suitable condition, and occasionally pays for the mistake with its life, owing to its ovipositor becoming firmly held by the tissues of the timber. The writer has, on more than one occasion, found the ovipositor with part of the insect attached, sticking in the bark of growing trees.

For successful oviposition, in the case of living trees, the limiting factors are transpiration and the activity of the cambium. In a tree with a large healthy crown and root system, transpiration is rapid, the sapwood consequently contains large quantities of water and the cambium is very active. Both these factors are inimical to the successful establishment of *Sirex* in the tree. Occlusion of the oviposition tunnel takes place rapidly and excess of water occurs ; the necessary air supply is not available for the successful hatching of the *Sirex* eggs and the development of the young larvae. This probably explains why a large crowned, wind-blown tree whose roots are still attached to the soil may be unsuitable for breeding purposes, while a similar tree which has been cut off and trimmed of branches may at once be successfully attacked. It frequently happens that some of the roots of a blown tree remain attached to the soil on one side, and when enough roots remain so attached, the vigour of the tree may be maintained for a considerable period, not, of course, at its original level, but at a level sufficiently high to render the tree unsuitable for *Sirex* for a season.

When felling operations were in progress during the summer, the writer on one occasion observed *Sirex* begin to oviposit in a felled larch even before the men had finished trimming off the branches, notwithstanding the fact that a few minutes previously the tree was quite unattractive. In this case the insect was evidently attracted by the odour from the freshly cut surfaces. Over-mature trees are always liable to attack and frequently suffer considerably.

While on the one hand, trees in a normal, vigorous state of health are not suitable as hosts for *Sirex*, the other extreme limit to the range of suitable conditions is reached when the cells of the timber are invaded by the mycelium of a fungus, other than the symbiont directly associated with the insect, or the timber becomes water-logged or decayed. Between these two extremes there is a wide range of conditions under which timber is suitable for successful attack.

Perhaps the least attractive trees are those which have been killed by excessive shade, but in this case it presumably is not the condition of the timber but the lack of light which deters *Sirex*. In the absence of other material more attractively situated, *Sirex* will attack trees which are heavily shaded. It sometimes happens that individual coniferous trees, particularly silver fir, which have grown in woods of broad-leaved species on long rotation, having attained a great height or developed some peculiar characteristic which gives them a sentimental value to the owner, are left standing when the surrounding trees are felled, or when very heavy thinnings are made in the woods. Often within a few years, owing to the exposure of the soil to the effects of sun and weather, and the consequent disintegration of the humus, the water-level in the soil is reduced and the trees are unable to obtain enough moisture to maintain the health and vigour of the large crown produced under more favourable circumstances. When this stage is reached, the trees begin to die back and become what is termed " stag-headed." In carrying out the large-scale collection of *Sirex* parasites in 1930–31, this type of tree provided very productive material. Trees with double leaders often lose one of the tops in a gale ; these tops were also very prolific in *Sirex* material. Trees killed or damaged by lightning, fire, felling or haulage operations, are also attacked. As already mentioned, larch felled in summer are particularly attractive. A larch plantation of about 20 years' growth was being thinned in Devon in August 1928. On the second day of the operations the writer observed several *Sirex gigas* adults ovipositing in small larch thinnings which had been felled the previous day.

During the winter of 1920 a large number of very fine larch trees were felled and the best trees were selected for telegraph poles. These poles were peeled by means of draw-knives during the summer of 1921. While this work was in progress the poles were attacked by *Sirex gigas* in considerable numbers.

It will be seen from the above observations that while certain conditions render timber unsuitable for *Sirex*, no peculiar pathological conditions are required to make the timber suitable.

The suggestion, which has frequently been made by writers on forest entomology during recent years, that *Sirex* and *Tetropium* may to some extent be regarded as beneficial, on the grounds that they call the attention of the forester to the existence of unsatisfactory conditions in the stand, is without foundation, since the presence of the sickly, dying or dead trees would be far more likely to attract the attention of the forester, and as has been shown above, *Sirex* often breed in material other than trees which are in a pathological condition. There is, perhaps, some justification for regarding *Sirex* as being somewhat useful, in common with *Rhagium* and *Asemum*, because they help to hasten the destruction and disintegration of useless material lying in the forest, and thereby facilitate its incorporation with the forest soil.

Under normal forest conditions, *Sirex* has never been known to become a pest in Britain. During the summers of 1937 and 1938, the writer spent several months in the pine forests of N.E. Scotland, and saw large areas of Scots pine up to 65 years of age which had never been thinned. Even in these areas *Sirex* is not very numerous on account of the control exercised by parasites, owing to the fact that in small poles the *Sirex* larvae are unable to burrow out of reach of *Rhyssa*.

When abnormal conditions arise, as for example in large windfall areas, where removal of the large trees is neglected, these conditions are exceptionally favourable for the increase of *Sirex* and considerable damage to the timber may result, but this is entirely due to the delay in removing or converting the large logs.

Conditions suitable for the increase of *Sirex* also occur where areas of forest are allowed to become water-logged and large numbers of trees become sickly and die.

Where normal felling operations are in progress the timber is seldom allowed to lie on the ground long enough to become seriously infested by *Sirex*, but in country sawmill yards logs can often be found which have been left lying neglected and have become the focus of a *Sirex* population.

Although *Sirex* cannot, under existing conditions in Britain, be regarded as a menace to the health or welfare of young coniferous crops, this would certainly not be the case in the absence of parasites. The chief limiting factor to its increase would then be the supply of suitable breeding material. All badly suppressed poles in a pine stand would be liable to attack and they would rapidly be reduced to a state in which they would be suitable for the breeding purposes of bark-beetles and other insects. This would result in an excess of suitable breeding material for these insects, thus upsetting the balance and turning the scale in their favour. They in turn would devastate the standing crops and provide fresh breeding material for *Sirex*. The insect would rapidly increase in numbers and would become a menace to nearly all coniferous timber, whether lying in the forest, stacked in timber yards or forming part of structures, unless adequately treated with preservatives before use.

So numerous are the parasites in *Sirex*-infested material, that it is difficult to find logs in which they do not preponderate. In 1935 the writer received a letter from Dr. E. A. Parkin of the Forest Products Research Laboratory, Princes Risborough, requesting him to supply *Sirex*-infested logs containing fully grown larvae and pupae, and as free as possible from parasites. He stated that some material he had received from Norfolk was, unfortunately, almost spoilt for his purpose by a positively enormous emergence of both *Rhyssa* and *Ibalia*. Since the receipt of Dr. Parkin's letter the writer has from time to time examined *Sirex*-infested logs, both in the New Forest and in the pine forests of N.E. Scotland, with the object of providing the desired material. In all cases, the material examined was found to be heavily parasitized.

It will be seen from the above observations that the status of *Sirex* in Britain is that of an insect under complete economic control.

This does not mean that *Sirex* is incapable of becoming a pest. Like every other species of insect which is capable of doing any kind of damage, *Sirex* would certainly become a serious pest were it not for the existence of the factors which keep it under control. In the case of *Sirex*, the writer is convinced that the parasites, *Rhyssa* and *Ibalia*, are by far the most important factors of control.

This view is not shared by all economic entomologists. In discussing " The Biological Control of Forest Insects," Professor J. W. Munro (1931) states : " Many other factors apart from animal parasites affect the well-being of insects, and the extravagant claims made by some entomologists in favour of parasite control cannot be accepted.

" The method, like all other methods, has its limitations, and it so happens that we know more of its limitations in forest entomology that in agricultural entomology. An important and valuable illustration of the inapplicability of parasite control is afforded by certain of the wood-wasps of the family SIRICIDAE."

Professor Munro doubtless selected this case as exhibiting with special force the weakness of the method of biological control as applied to forest entomology. It is therefore necessary to consider his arguments very carefully in order to scertain whether his statement is substantially correct.

Professor Munro sets out to discuss the question of the introduction of parasites into New Zealand with the object of controlling *Sirex*, but the whole argument circles round the question of the desirability or otherwise of introducing parasites into Tubney Arboretum, Oxford.

After producing hypothetical reports by two fictitious investigators, one a forester and the other an entomologist, he concludes by saying " Here then is an instance where control by parasites is not only impracticable but wrong-headed."

Professor Munro's argument is based on the assumption that the occurrence of *Sirex* is governed by the existence of conditions favourable for the growth of its symbiotic fungus, *Stereum*, the vital factor being a peculiar pathological condition produced in timber by death through water-logging of the soil, and the attack of the fungi, *Fomes annosus* and *Armillaria mellea*. Before producing the imaginary reports of the forester and the entomologist, he is careful to state " The fungi *Fomes annosus* and *Armillaria mellea* are found on many of the trees, but not both together."

Both the reports are based on the data thus provided. The forester mentions the presence of *Tetropium* as confirming the existence of the pathological conditions and incidentally rendering the occurrence of *Sirex* tertiary.

Before we can accept Professor Munro's explanation of the conditions governing the occurrence of *Sirex*, it will be necessary to verify certain rather important details. For example, the presence in the area of the two fungi, *Fomes annosus* and *Armillaria mellea*, is of vital importance if they are to play their important part in the production of the hypothetical pathological conditions which favour the growth of the symbiotic fungus *Stereum*.

When introducing his mythical entomologist, Professor Munro says " If he is good at his work he will begin with a study of the literature." If he himself had followed this excellent advice, he would have discovered the following statement in Dr. Chrystal's paper " The *Sirex* Wood-wasps and their Importance in Forestry " (1928) :—

Field Studies in Tubney Wood, Oxford.

" Through the kindness of Mr. W. R. Day, Mycologist to the Imperial Forestry Institute, I was able to make a survey of the wood in company with him to collect data on the following points :

(1) The general condition of the larch and its relation to soil conditions, silvicultural treatment, etc.

(2) The presence of root fungi as antecedent to, or contemporary with, the *Sirex* attack.

" Two root fungi were looked for, *Armillaria mellea*, the honey fungus, and *Fomes annosus*. On a previous preliminary survey it was thought that one or both these fungi might be prevalent, causing primary injury. After searching both in the field and in the Laboratory, however, no sign of the rhizomorphs of *A. mellea* or of the mycelium of *Fomes* could be traced.

" On the other hand extensive root rot was present, the tap-roots of many trees being completely destroyed. This was entirely due to the waterlogged condition of the soil."

It appears, therefore, that Professor Munro's theory is without foundation, since it was built up entirely on the assumption that the two fungi were present in the area.

It is true that Dr. Chrystal does, in one or two of his papers, refer to *Sirex*-infested silver fir which had been killed by these fungi. These records do not, however, refer to Tubney Aboretum, but to some plantations in North Devon which he visited with the present writer in 1928.

The fact that no one has ever suggested the introduction of parasites into Tubney Arboretum, or even hinted that *Sirex* was a pest in that area, is of little importance.

Dr. Chrystal has shown that both *Rhyssa* and *Ibalia* are fairly numerous at Tubney, and presumably in order not to deplete the *Sirex* population there, which he required for his own studies, on 23rd November, 1928, he addressed a letter to the present writer asking him to collect as many living *Sirex* larvae as possible in Devon, as he was anxious to get these to send to a colleague in the north who was going to undertake a cytological study of them.

In discussing biological control, Professor Munro states : " The principle of the method in its simplest form is, briefly, that excessive increase of insects is caused by lack of natural enemies, of which parasitic insects are the most important, and that the best method of restoring the balance and of reducing the noxious insects to numbers which are harmless is to introduce to the areas affected large numbers of the parasites.

" If the premises are right and the increase of a noxious pest is the result of the absence or paucity of insects parasitic on it, the logic of the method is unassailable, and it is noteworthy that where these conditions hold, the success of parasite control is assured."

These are precisely the conditions which exist in New Zealand.

7. The Present Status of Sirex in New Zealand.

The following account of the present status of *Sirex* in New Zealand is taken from a paper written by Dr. D. Miller (1935), Chief Entomologist at the Cawthron Institute, and Mr. A. F. Clark, Forest Entomologist, State Forest Service, and is reproduced here because it constitutes an authentic statement of the conditions which exist, written by the men who are actually in charge of the operations in connection with the biolgoical control of *Sirex* in New Zealand ; also because the statement forms the foundation on which the present writer bases his conclusions on the discussion which follows.

" Although on the whole our plantations of exotic conifers, now amounting to some 500,000 acres, have not yet suffered from widespread epidemics, there are certain exotic insects already well established in the country that must be considered as potentially dangerous. Attention is being given to the most important of these.

" One species, though not a serious pest of healthy trees, has attracted considerable attention owing to its widespread establishment throughout the Dominion. This is the steel-blue horntail-borer or wood-wasp, *Sirex noctilio*, of Europe, which in this country attacks *Pinus radiata*, *P. laricis*, *P. muricata*, *P. austriaca*, *P. pinaster* and *Larix europaea*, whilst on one occasion it was found attempting to oviposit in the native Miro (*Podocarpus ferrugineus*). Attacking suppressed, dying and dead trees for the most part, this insect is nevertheless an important factor detrimental to forest protection since it may hasten the death of trees that could be utilised, as well as creating conditions favourable to the breeding of the European bark-beetle (*Hylastes ater*, Payk.) now well established in many regions. In this respect it is of importance to note that some large commercial concerns which have extensive pine forests, apparently intend to attempt the management of these upon a sustained yield basis with an extremely short rotation by a system of clear felling at the age of 12 to 16 years and subsequent replanting. Exotic conifers, maturing very rapidly in New Zealand, present ample pabulum for the larvae of *Sirex* at the above mentioned ages, and the stumps of such trees attacked by that insect and infested with *Hylastes*, will, after clear felling, be centres from which *Hylastes* will spread and attack the fresh crop of seedlings, as has already been the case. Further, since exotic conifers have been planted somewhat indiscriminately all over the land, often without due consideration of site, some areas, having reached a fairly advanced state, appear to be weakening and becoming susceptible to *Sirex* attack. A further factor contributing to the development of *Sirex* is the lack of suitable plantation management. The basic difficulty is usually the fact that thinning, instead of yielding an intermediate return, such as might be expected under Old World conditions, is in such cases a definite additional capital charge, since small sizes of the timbers grown can only on rare occasions be profitably utilised. It is, therefore, not surprising that the average plantation owner avoids thinning, even when he realises that trees have to be farmed, as has any other crop, with the result that suppressed, broken, and dead trees comprising dense thickets are common.

" Although suppression, breakage, and poor site are the most frequent causes inducing *Sirex* attack, the influence of fire and fungi cannot be overlooked.

"Very few plantations, outside those owned by the State and large commercial concerns, are adequately protected from fire, and it is no uncommon sight to see a considerable area of valuable trees irreparably damaged by accidental fires; this is particularly so when the plantations are situated along main highways or in the vicinity of settlements. Fire-killed trees, provided they are dried out, are not favourable for the breeding of *Sirex*, but in the case of light ground fires which cause the tree to wilt and die gradually, the insect finds an excellent breeding ground . . . . *Sirex noctilio* has been present in the Dominion for a considerable time; as far back as 1900 the insect was found in the Waiarapa district of the North Island. For many years it was by no means a common species, but with the development and extension of areas under exotic conifers it has correspondingly increased and is now one of the commonest species met with amongst our insects of economic importance."

Although it is at least 38 years since *S. noctilio* first became established in New Zealand, the insect has not yet become distributed throughout the whole country. This is an important fact, as it indicates the urgent necessity for dealing effectively with the insect without delay so as to localise the sphere of operations and if possible to restrict its distribution. It must be remembered that although the spread of the insect would, in the early stages be very slow, every year must witness a great increase in the area of infestation, owing to the rapidly increasing population spreading out over a much wider radius each year. The full extent and nature of the damage which *Sirex* is capable of causing will not be realised until a point is reached when further distribution is impossible. Owing to the strong powers of flight and very active habits of the adult insect, the present process of distribution tends to keep down the density of the population in any particular locality.

The rate of spread during the last few years cannot be regarded as a standard of comparison for the distribution during a similar period in the future. In all probability during the next few years *Sirex* will have become established in all coniferous stands throughout the country.

Once the possible range of distribution has been reached there will be a spontaneous increase in the density of the population. If, for example, in say the year 1945 there is an average of 100 female *Sirex* per acre, the next generation arising from these insects could, in the absence of natural enemies, number 40,000 per acre, since the biotic potential is 400 per female. If this stage is ever reached *Sirex* will have become a menace to the existence of the entire coniferous forest. Unfortunately the rate of progress of the spread of the insect is not easily seen as, unlike leaf-eating insects, the larvae develop out of sight and the adult insects are mostly hidden away in the forest and are not very conspicuous when not in flight.

The apparent scarcity of adult insects in any particular year must not be taken as an indication that the infestation is on the decline, because as *Sirex* normally has a three year life-cycle, major flight years might occur at intervals of three years, but as the life-cycle may sometimes be completed in two years, and under certain conditions may be extended to four or more years, the progeny of these exceptional cases get out of step and appear during the years forming the intervals between the main flight years. Periodicity of the flight years is, however, not so marked in the case of *Sirex* as with such insects as cockchafers, because the development of the latter is largely influenced by climatic and physical conditions affecting the temperature and moisture of the soil, and by cultural methods and crop rotation. These factors exercise little influence on the rate of the development of *Sirex*, since the insect develops in an entirely different medium.

Dr. Miller and Mr. Clark have pointed out that the clearance of large areas of pines on a short rotation will have the effect of providing a continual succession of fresh breeding-places for *Hylastes ater*, from which these insects will spread and attack the fresh crops of young trees. It might also be mentioned that these beetles will also attack the roots of suppressed trees in the older stands for breeding purposes and bring about their death, thus providing additional breeding material for *Sirex*. *Hylastes* may even attack and kill trees which are not badly suppressed, as sometimes occurs in Britain. Indeed this is very likely to happen where the insect is very numerous. It will be seen, therefore, that although *Hylastes* and *Sirex* belong to entirely different orders, they form a definite biological association of a particularly dangerous type, and their combined activities may, in favourable circumstances, result in the formation of a vicious circle.

8. The Introduction and Establishment of Rhyssa in New Zealand.

A short account of the collection of 7,830 *Rhyssa* larvae for shipment to New Zealand has already been given. The following account of the importation and liberation of the insect is based on a paper by Dr. Miller and Mr. A. F. Clark (1935), who were in charge of the work in New Zealand.

" Owing to the abnormal abundance of *S. noctilio* in the plantations of exotic conifers, steps were taken in 1927 to locate and introduce a parasite for its control. Adverse opinions were expressed upon the venture, since it was assumed that any attempt to introduce and establish a parasite of a wood-boring insect would fail. Why this should be so in the case of wood-boring parasites more than in the case of other insects, we failed to see ; and as the results to date have shown, the assumption was unfounded and demonstrates that one cannot definitely foretell the success or failure of any project connected with the biological control of insects.

" The importation of *Rhyssa persuasoria* was carried out between December 1928 and April 1929, and again between March and August 1931 ; during these periods nineteen consignments, totalling 7,830 individuals were sent us from Farnham Royal.

" The insects were shipped in the larval stage under cool storage conditions, and packed in gelatin capsules or corked glass tubes, a single larva to each receptacle. In some cases larvae had pupated and in others adults developed during the voyage.

" Some 160 parasite larvae of the 1928–29 consignments were sent in glass tubes, but in all other shipments gelatin capsules were used. The glass tubes were not a success, owing to the accumulation of moisture and the development of mould upon the larvae. Many of these mould-affected larvae were saved by brushing with a very fine brush dipped in a saturated solution of boracic powder in cold water. This treatment was effective in removing the mould and allowing about 40 per cent. of the infected larvae to pupate, but the adults emerging from these were in poor condition. The capsules and tubes of the 1928–29 consignments were packed in cottonwool and those of 1931 in sawdust ; both methods gave equally satisfactory results, though the sawdust apparently ensured more suitable conditions of moisture and temperature. In some cases sawdust was placed in the capsule with the insect, but no marked difference resulted."

The data furnished by Dr. Miller in his description of the state of the parasites in the various shipments on arrival in New Zealand are reproduced below. The living individuals are marked (+) and dead or diseased (—).

The data reveal a high rate of mortality during transit, a very unsatisfactory state of affairs, particularly in the case of insects which are so extremely difficult to collect in large numbers. This high rate of mortality is a matter of great importance, and the cause should be ascertained if possible. The data must, therefore, be examined in detail.

The first two shipments containing 201 parasites were received on 8th December, 1928, and 7th January, 1929. They were all in the larval stage on arrival and the total mortality was only 2·98 per cent.

The third and fourth shipments received on 9th and 15th January contained 460 parasites. On arrival 13 pupae were found in these shipments, showing that

Particulars of Shipments received during 1928–29.

Consignments	Received	No.	Condition on arrival			
			Larvae	Pupae	Adults	Percentage Alive
1st	8.xii.28 ...	51	47 (+) 4 (−)	—	—	92·16
2nd	7.i.29 ...	150	148 (+) 2 (−)	—	—	98·66
3rd	9.i.29 ...	143	111 (+) 31 (−)	1 (+)	—	78·32
4th	15.i.29 ...	147	120 (+) 15 (−)	12 (+)	—	89·75
5th	12.ii.29 ...	100	45 (+) 42 (−)	9 (+)	4 (+)	58·00
6th	14.ii.29 ...	147	57 (+) 29 (−)	5 (−)	56 (−)	38·77
7th	20.ii.29 ...	228	78 (+) 23 (−)	16 (+)	52 (+) 59 (−)	64·03
8th	7.iii.29 ...	207	82 (+) 56 (−)	2 (+)	67 (−)	40·57
9th	13.iii.29 ...	184	89 (+) 26 (−)	5 (−)	13 (+) 51 (−)	55·43
10th	14.iv.29 ...	96	37 (+) 11 (−)	7 (−)	3 (+) 38 (−)	41·66

Particulars of Shipments received during March and April, 1931.

Consignments	Received	No.	Condition on arrival			
			Larvae	Pupae	Adults	Percentage Alive
11th	6.iii.31 ...	610	515 (+) 43 (−)	52 (+)	—	92·95
12th	19.iii.31 ...	690	568 (+) 36 (−)	86 (+)	—	94·87
13th	24.iii.31 ...	556	392 (+) 31 (−)	133 (+)	—	94·42
14th	8.iv.31 ...	248	135 (+) 45 (−)	68 (+)	—	81·85
15th	13.iv.31 ...	337	251 (+) 35 (−)	51 (+)	—	89·32
16th	21.iv.31 ...	1,200	966 (+) 39 (−)	195 (+)	—	96·75
17th	14.iv.31 ...	1,043	696 (+) 100 (−)	247 (+)	—	90·41
18th	16.iv.31 ...	1,242	813 (+) 200 (−)	229 (+)	—	83·09

Particulars of Shipment received during August, 1931.

Consignments	Received	No.	Condition on arrival			
			Larvae	Pupae	Adults	Percentage Alive
19th	6.viii.31 ...	451	233 (+) 112 (−)	105 (+)	1 (+)	75·12

development was rapidly taking place. The mortality was 15·86 per cent. In all the other shipments, totalling 962 parasites received between 12th February and 14th April, 1929, adult insects were found. The material in these shipments may, therefore, be regarded as being in much the same state of development. The total mortality for these six shipments was 49·38 per cent.

These figures show that the mortality increased in direct ratio to the advance in state of development of the parasites at the time of their arrival, and probably, therefore, their collection and shipment.

The rate of mortality for the various stages in which the parasites in the last batch of shipments arrived, confirms this view. The figures are as follows :—

Larvae =32·52 per cent. mortality.
Pupae =38·64 per cent. mortality.
Adults =79·01 per cent. mortality.

Mortality among the adults was probably due to starvation, but this would not have occurred if all the material had been shipped early enough to arrive in the larval stage. It is unfortunate that these data were not available before the 1931 collections and shipments were made, as the figures clearly indicate the desirability of making early collections so as to get the larvae delivered before metamorphosis takes place.

It will be seen that the whole of the 1931 shipments contained no adults on arrival, although they all contained pupae. In this respect they resemble the stage of development found in shipments 3 and 4 in the 1929 collections, and as in the case of those two shipments, there is no mortality among the pupae. The total mortality of the 1931 shipments 11 to 18 is only 8·93 per cent., but this is much higher than is desirable.

The absence of adults in the 1931 shipments, although they were received at dates corresponding to the last 3 shipments of 1929, is accounted for by the fact that the majority of the parasites in 1931 were collected at an altitude of 1,000 ft. in a very exposed area in Montgomeryshire, during a spell of very severe weather. On the other hand, the whole of the 1929 collections were made at fairly low elevations in rather sheltered situations in Devonshire. It will be seen, therefore, that the development of the 1931 parasites would be considerably retarded as compared with that of the parasites in 1929. In fact, during 1929 some pupae and adults were found in the logs examined in the forest during the time of collection.

The 19th shipment received on 6th August, 1931, shows a mortality of 24·83 per cent. This is accounted for by the fact that the collection had been kept in the refrigerator at Farnham Royal throughout the summer. The mortality in this shipment compares favourably with that of the last six shipments of 1929.

Considering the enormous expenditure of labour and patience involved in the collection of these relatively scarce parasites, the importance of reducing the mortality during transit to a minimum is of the utmost importance, and the above analysis of the data emphasises the necessity for closer co-operation between the persons in charge of importation and liberation, and those responsible for the collection and shipment of the material.

Unfortunately, mortality during transit was not the only source of loss. A matter of even greater concern is the fact that a large proportion of the surviving females emerged with deformed ovipositor. In discussing this matter Dr. Miller and Mr. Clark (1937) state " The main difficulty encountered in New Zealand in connection with the establishment of *R. persuasoria* was the malformation of the ovipositor of the females in the case of insects which had been shipped from England. The reason for this malformation was never clearly demonstrated ; the larvae appeared perfectly healthy, the resulting pupae were large in most cases and well formed, but in many instances the adult emerged with the ovipositor so deformed that egg-laying was impossible. While a certain amount of success was obtained by artificial adjustment immediately after the adult emerged, out of the total of nearly 8,000 insects imported only 179 females were liberated."

The above remarks indicate that the actual loss of material due to malformation of the ovipositor of the females was of even greater importance than the loss sustained through mortality during transit. Malformation of the ovipositor is not a common occurrence under normal conditions in the forest. In fact the writer has not observed such an occurrence except in the case of specimens reared in capsules, and as Dr. Miller has pointed out in discussing the rearing of *Rhyssa* in New Zealand, " In no case was other than a perfect insect produced." It may, therefore, be reasonably assumed that deformity of the ovipositor is either the result of removal of the larva from the normal pupal chamber and transfer to the artificial pupal chamber, or the result of injury sustained during transit.

Under normal conditions, when fully grown, the *Rhyssa* larva spins a thin silken cocoon which lines the pupal chamber. In the majority of cases this cocoon had already been spun before the *Rhyssa* larvae were collected. In such cases, when transferred to a gelatin capsule, the adult insect on completing its development is enclosed in a pupal chamber with perfectly smooth sides which afford no foothold, and in consequence the insect is caused to struggle violently before it succeeds in biting its way out. This may result in causing the ovipositor to become twisted out of shape before it is sufficiently hardened, or the delay in affecting an exit may result in the ovipositor becoming hardened before it has become straight and assumed the position it normally occupies when ready for use. On the other hand, the deformity may be a direct result of the jolting which takes place during transit. In either case the difficulty could probably be overcome by collecting the larvae before they have spun their cocoons, thus allowing them to spin the cocoon inside the gelatin capsule, in which case exit of the adult would be greatly facilitated. The cocoon would also to some extent absorb the shock of jolting in transit. Another important point in this connection is the paying of greater attention to selecting a capsule of suitable size for each larva, so as to reduce the space in which it is tossed about during the journey through the post to the laboratory and during reshipment.

This is a point to which insufficient attention was paid owing to the fact that no one had previous experience in shipping such a large wood-boring parasite.

It seems probable that by early collection of the larvae and greater attention to their individual requirements in packing for shipment, and during the pupal period, mortality during transit and malformation of the ovipositor may be almost entirely eliminated.

In describing the establishment of *Rhyssa* in New Zealand, Dr. Miller and Mr. Clark say " The liberations were made during the years 1929, 1931 and 1932, in seven districts in the South Island, and two districts in the North Island. The rearing of the parasite was first undertaken in the insectary in 1931 and carried on with success. To date four New Zealand generations have been reared, and small liberations have been possible at Rotorua and in other districts. However, the total number of females placed in the field did not reach 200.

" It is not surprising that, although favourable reports were received from many observers for several years, the writers were unable to check and record the definite establishment of *R. persuasoria*. The small number of insects liberated and the large area of forest, presented very severe handicaps to recovery. The success of insectary rearings, however, pointed to the probability that establishment had taken place. This season, however, the recovery of *R. persuasoria* has been made in two districts in the South Island. Pine logs brought into the insectary from the Moutere District, Nelson, yielded the parasite, and one tree felled at Hanmer Springs and kept under caged conditions yielded several males and females.

"The strong establishment of the parasite at Hanmer Springs is particularly pleasing, as this is a large plantation area and provides ample breeding material."

Although several hundred larvae of *Ibalia leucospoides* were collected no attempt has been made to establish this species in New Zealand. A shipment was made but the material did not arrive in a satisfactory condition and Dr. Miller decided to concentrate on *Rhyssa*, at any rate until the latter had been successfully established. It is felt that the difficulties in connection with the transportation of *Ibalia* can easily be overcome and that the insect can be delivered in sufficiently large numbers if required.

The establishment of *Ibalia* will be rather more difficult than in the case of *Rhyssa* owing to the fact that it will be necessary to synchronise the emergence of the *Ibalia* adults with the period of oviposition of *Sirex*. This, however, should present no serious obstacle since the oviposition of *Sirex* extends over a considerable period, and the last larval stage of *Ibalia* extends over a complete year. This will allow considerable latitude for either the acceleration or retarding of development.

The question of the desirability of introducing *Ibalia* is, however, one which will require careful consideration. It has been shown that both parasites are very efficient; each can produce a high percentage of parasitism, and their combined attack results in a higher percentage of parasitism than when each parasite is separately concerned.

Rhyssa is intrinsically superior to *Ibalia* and super-parasitism of the latter by the former is of very frequent occurrence. This has the effect of inflating the figures showing the percentage of *Rhyssa* at the expense of *Ibalia*, as every case of super-parasitism or hyper-parasitism by *Rhyssa* represents a duplication of work which has already been accomplished by *Ibalia*. On the other hand every *Ibalia* adult that emerges represents the destruction of a *Sirex* larva which has escaped parasitism by *Rhyssa*, and as *Ibalia* is incapable of destroying *Rhyssa*, the evidence appears to be all in favour of the introduction of both species.

The problem is not, however, so simple as the above facts seem to indicate. *Rhyssa* is extremely variable in size, the largest specimens the writer has found in Britain were just over 3 inches in length. Of this, slightly more than half represents the ovipositor. These specimens were bred from *Sirex gigas* hosts, smaller hosts produce smaller *Rhyssa* adults. When *Ibalia*, or a *Sirex* larva parasitized by *Ibalia*, is the host, the resulting *Rhyssa* adult is extremely small and the ovipositor is correspondingly short (often less than $\frac{1}{2}$ inch in length), is incapable of penetrating very far into the timber, and in consequence has a very limited range of usefulness. Owing to the superficial position in the timber occupied by *Ibalia* larvae and *Sirex* larvae parasitized by *Ibalia*, it seems probable that they will be more susceptible to parasitism by *Rhyssa* than *Sirex* larvae which have escaped parasitism by *Ibalia*, as the latter burrow deeper into the timber. It seems, therefore, that the more numerous cases of parasitism by *Ibalia* become, the greater will be the number of very small *Rhyssa* adults. In the case of a *Sirex* population which is under control at a low level, where control is facilitated by the small diameter of the available breeding material, the size of *Rhyssa* is obviously a matter of little importance, since the size is to some extent automatically maintained by the fact that small adult parasites can often reach large host larvae, thus giving rise to large offspring.

With a rapidly increasing *Sirex* population and an adequate supply of breeding material of larger diameter, as is the case in New Zealand, the position may be entirely different. In this case the size of the parasite and corresponding length of ovipositor is of great importance, because a large parasite with a long ovipositor is doubtless more efficient than a small parasite with a short ovipositor.

The problem is, therefore, whether the margin of effective parasitism attained by *Ibalia* would more than compensate for the reduction in the efficiency of *Rhyssa*.

There is a possibility that the efficiency of *Rhyssa* might deteriorate to such an extent that its status would be reduced to the equivalent of a hyper-parasite and consequently cause a corresponding reduction in the efficiency of *Ibalia*.

Another point which ought to be investigated before any attempt is made to introduce *Ibalia* is the question of whether the reduction in size of the *Rhyssa* adult, either directly as a result of feeding on a small host, or indirectly through super-parasitism or hyper-parasitism, has any effect on the reproductive capacity of *Rhyssa*.

On the other hand there does seem to be a possibility of utilising *Ibalia* to fill an ecological niche. There appears to be some evidence that *Ibalia* is more numerous in larch timber than in silver fir or spruce. This may be because of the flaky nature of larch bark, possibly because the flakes of larch bark tend to deflect the ovipositor of *Rhyssa*. If this is found to be the case, the same would probably apply to Corsican pine, in which case it might be worth while establishing *Ibalia* alone in pure stands of these species. It is, however, a matter for further investigation.

The net results of the investigation started in 1927 can be stated as follows :—

(1) It has been shown that the parasites of *Sirex* can be collected in large numbers at relatively low cost, notwithstanding the fact that both *Rhyssa* and *Ibalia* were both formerly regarded as being very rare insects. In fact practically nothing was known about the latter.

(2) The biology and post-embryonic development of *Ibalia* has been studied in great detail by Dr. R. N. Chrystal at Oxford, and the results of his researches have been published.

(3) Field studies on the ecology and economic status of *Sirex*, and the inter-relationship of the insect and its parasites have been carried out on a large scale by the present writer, and considerable experience has been gained in the technique of collecting and shipping the parasites.

(4) Dr. D. Miller and Mr. A. F. Clark have succeeded in definitely establishing *Rhyssa* in New Zealand, and specimens have been recovered in the forest several years after the liberations.

It will be seen, therefore, that the investigation has had positive results. However, even the most enthusiastic advocate of biological control would not suggest that the liberation of one female parasite for each 2,500 acres of *Sirex*-infested forest could have any appreciable control effect on the population of a host with a biotic potential of 400, and a standing of over thirty years establishment ; and no practical consequences can be expected until the population of *Rhyssa* has increased to a point where it is comparable with that of *Sirex*, which may take many years. It might however, be possible to accelerate the process if further large-scale importations of the parasites of *Sirex* were made, since they could then be widely established over the whole of the infested area.

9. Methods of Control.

The foregoing excellent description by Dr. Miller and Mr. Clark of the conditions existing in the forest in New Zealand conveys to the mind of anyone conversant with the various species of trees and insects concerned a mental picture forming a background against which the possible methods of control may be considered.

Apart from the encouragement of birds and any other useful predators which may be present, it is obvious that some method of controlling the increase and spread of *Sirex* will have to be adopted if the insect is to be prevented from becoming a serious pest. These control methods may be considered as follows—(*a*) Silvicultural and mechanical control ; (*b*) biological control.

(*a*) *Silvicultural and Mechanical Control.*

During recent years frequent references have been made to the application of silvicultural practice in regard to the control of forest insect pests. Many of the statements are of an extremely vague character and give not the slightest indication as to what is meant. If it can be shown that any particular silvicultural operation can be carried out in such a way as to benefit the crop directly, and at the same time indirectly by helping to control insects which are detrimental to the crop, it is clear that full advantage should be taken of such an opportunity.

The choice of silvicultural system and the formation of mixed or pure stands, correct selection of site and situation for the various species concerned, length of rotation, arrangement of working circles and felling series, are subjects thoroughly understood by all officers in charge of State forests, and should also be understood by the forest entomologist, so that, in consultation, working plans can be so arranged as to afford the greatest possible measure of protection against insect damage and facilitate the control of the insect population, special rules being formulated to deal with any particular operation and its effects concerning any given species of insect. There is, however, a limit to what can be done in the way of insect pest control by silvicultural means, even if the whole of the forests concerned are directly under the jurisdiction of the forestry department. But when considerable areas of privately owned forest exist, the efforts of the forestry department are liable to be vitiated by neglect on the part of adjoining owners. It is, therefore, of the utmost importance that every effort should be made to enlist the co-operation of private owners.

It is clear that little can be done in New Zealand to control *Sirex* by means of change in silvicultural system, and there is no evidence to indicate that *Sirex* is less numerous in mixed woods than in pure coniferous stands in Britain. In any case half a million acres of coniferous plantations have already been established in New Zealand, and it is in these areas that the control of *Sirex* must be undertaken.

It has sometimes been stated that the increase of wood-boring insects and bark-beetles is determined by the amount of the available food supply. If this statement were true, *Sirex* would be extremely abundant in many of the unthinned pine forests in N.E. Scotland and in many parts of Europe, but such is not the case, although in the absence of the existing parasite population it seems probable that such a state of affairs would exist.

The popular impression that *Sirex* could be controlled in New Zealand by thinning operations is a fallacy. Much can be done by destroying the insects in certain areas from time to time, but this would not result in the control of the species.

Normal thinnings are only carried out as and when necessary, and the correct time is determined by the silvicultural requirements of the crop. A proportion of the suppressed trees must always be left standing in order to preserve the required density of the stand and maintain an unbroken canopy. Some of these suppressed trees would become suitable for breeding purposes within a very short time, and would doubtless be used for that purpose.

The frequency of normal thinnings is determined by the density of the stand and the rate of growth of the trees. This may differ for each species of tree, and is influenced by differences in soil and situation. As Dr. Miller and Mr. Clark have pointed out, the rate of growth of pines in New Zealand is exceptionally rapid. This means that the silvicultural requirements of the crop will demand light and frequent thinnings. The more rapid the growth of the crop, the sooner do suppressed trees become suitable for the breeding purposes of *Sirex*, and in order for the thinning operations to have any effect on the *Sirex* population the thinnings would have to be carried out at very short intervals, probably every five years. This would mean a thinning programme of 100,000 acres each year, the cost of which would be chargeable to the maintenance of the crop. These extensive thinning operations would inevitably result in a huge surplus of unsaleable material, which would be most abundant in the more remote areas. Normal silvicultural requirements would not necessitate the removal or destruction of this unsaleable material and it could with advantage be left on the ground to rot, but as a control measure for *Sirex* it would be necessary to collect and destroy it. Even at an average cost of £1 per acre this additional expense would amount to £100,000 per annum and would represent the cost of *Sirex* control. This would be a recurring charge and there would be no guarantee that it would have the effect of controlling *Sirex.*

Little can be done by way of mechanical control, but the following method would produce some result. Fresh-felled poles stacked against trestles in open places in the forest attract *Sirex* for oviposition. These poles should be destroyed late in the season after the eggs of *Sirex* have been laid in them.

The collection of eggs and destruction of breeding material can only be regarded as palliatives, and in the opinion of the writer they largely constitute a waste of public funds, as the process would have to be continued indefinitely.

(*b*). *Biological Control.*

Critics of biological control seldom take the trouble to ascertain what really are the factors which exercise control over insects during normal periods. Their observations are often based on exceptional cases, where, for one reason or another, the balance has been upset and an outbreak has occurred. Under such conditions it is quite clear that control is not, for the time being, in operation, but it is equally clear that abnormal circumstances such as these should not be used as a criterion. The proper time to collect evidence of control is during the period when control is actually in operation.

In cases where control has temporarily broken down, from whatever cause, it is generally necessary to adopt some form of artificial control in order to reduce the insect population as speedily as possible, to prevent excessive damage to the crop. Such control measures are generally expensive and can, as a rule, be used only as expedients ; the extent of their use generally being determined by the value of the crop. When certain crops are being grown in conditions under which they are known to be prone to excessive insect damage, it is often possible to prevent such damage by the use of chemicals. When such circumstances exist the most enthusiastic exponent of biological control would not hesitate to prescribe chemical treatment. Similarly under certain other conditions he would advocate mechanical control, such as various forms of trapping. All economic entomologists recognise that each of the methods of control must have their proper place if a complete system of pest control is to be established. No sane person has ever suggested that parasites are the only factors of control under all circumstances, and as has already been pointed out in the preceding pages, although one set of factors may normally be responsible for the control of an insect, quite a different set of factors may come into operation when abnormal conditions arise ; for example, parasites, predators, and other factors, operating in a block of unthinned pine forest may so effectively check the increase of the bark-beetle population under normal conditions that the insects are unable to become sufficiently numerous to cause appreciable damage. While this stage continues the bark-beetles are under economic control and these conditions may continue over a long period of years, the duration of the period being largely determined by the rate of growth of the crop. But if extensive wind-falls occur, or heavy felling operations are carried out, facilities for the rapid increase of the bark-beetle population occur, the beetles are able to distribute their egg galleries over a much larger area of exceptionally suitable breeding material, and the resident population of parasites and predators is inadequate to deal with the sudden change in circumstances. Under these changed conditions it is necessary to undertake energetic mechanical control measures.

The above illustration may appear to support the statement that the increase of the beetle population is governed by the amount of the available food supply, but the important point is that under normal conditions the beetles are kept in check by the parasites and predators, and it is the sudden increase of exceptionally suitable breeding material in the form of thick-barked timber that turns the scale almost entirely in favour of the beetles and results in upsetting the balance. This does not detract from the importance of the parasites and predators as control factors under normal conditions.

Similarly in the case of *Sirex*, control by parasites in an unthinned pine stand of say 50 or 60 years may be sufficiently complete to prevent an increase of the host insect, but if a few logs of large diameter are left lying about, these logs will provide exceptionally suitable conditions under which a large proportion of the *Sirex* larvae may escape parasitism by *Rhyssa*, and an increase in the *Sirex* population will follow. If the additional favourable breeding material is sufficiently abundant it will inevitably result in an outbreak of *Sirex* and the status of the insect as a pest will be determined by the amount of timber which has been ruined. Here again it will be seen that the parasites are efficient factors of control under normal forest conditions ; the host only becomes a pest when exceptionally favourable conditions are provided for its increase. When, however, there are no parasites to keep its increase in check, *Sirex* will become a pest under normal forest conditions.

Dr. Miller and Mr. Clark have drawn attention to the fact that large areas of coniferous trees are being grown in New Zealand on exceptionally short rotation and that the thinnings, instead of yielding a return, are a definite additional capital charge, and that the average plantation owner avoids thinnings on account of the small material being unsaleable, with the result that suppressed, broken and dead trees comprising dense thickets are common. These conditions are mentioned as an illustration of the difficulty in carrying out mechanical control of the insect.

Fortunately these are exactly the conditions which provide the maximum facilities for the increase of *Rhyssa*. It is in material of this description that the highest percentage of parasitism is found in Britain.

Similarly the numerous stumps resulting from the felling of these young plantations are referred to as forming centres from which *Hylastes ater* will spread and attack the fresh crop of young trees. Here again, the conditions are ideal for the rapid increase of the various species of *Rhizophagus* and other predators. An attempt to establish the predators of *Hylastes ater* has been made on a very small scale. *Rhizophagus ferrugineus*, *R. dispar* and *R. depressus*, to the number of 3,711 were shipped from Farnham Royal to New Zealand. Dr. Miller and Mr. Clark (1935) record the liberation of 865 specimens. As this works out at less than 1 pair of predators for each 1,000 acres of coniferous plantation, the liberation can only be regarded as an experiment in attempting to establish the insects and not, at present, as a typical example of the method of biological control. It has been pointed out that *Hylastes* and *Sirex* form a biological association of a very dangerous type, and their uncontrolled activities are certain to have disastrous results in extensive coniferous plantations. Notwithstanding the fact that statements have been made to the contrary, both these species are normally controlled almost entirely by their natural enemies in Britain, and as both pests have become firmly established in New Zealand, the absence or scarcity of their natural enemies will undoubtedly result in tremendous damage to the coniferous crops unless adequate steps are taken to introduce their natural enemies in numbers sufficient to deal with the situation. This would mean the liberation of parasites and predators by the hundred thousand, and it could be accomplished at relatively little cost. The expenditure of the sum of one penny per acre of coniferous forest would be sufficient to cover the cost of carrying out a comprehensive scheme of biological control that would ultimately result in reducing both *Sirex* and *Hylastes* to be desired level of economic control which these insects normally occupy in Britain. As Mr. A. F. Clark (1936) has stated : " The introduction of parasites for the control of the wood-wasp was, and is, necessary, for the very good reason that the essential silvicultural measures are not possible in many cases for economic reasons."

10. Summary and Conclusions.

1. The ecological study of *Sirex* and its parasites was begun in 1927 and continued while making large-scale collections of the parasites for shipment to New Zealand with the ultimate object of the control of *Sirex noctilio*, a species of wood-wasp which has been established in the Dominion for many years.

2. A brief outline of the life-cycle of *Sirex* and the parasites is given. The difference in the method of attack by the parasites on the host is described, and some points of interest in connection with insect behaviour are discussed.

3. The methods of collection are described and particulars given about the number of parasites collected.

4. The inter-relationship of the host and parasites is discussed. It is shown that a single generation of *Sirex* can support three generations of *Rhyssa* and one generation of *Ibalia*, and that the effects of parasitism by *Rhyssa* are cumulative. The percentage of parasitism by *Rhyssa* cannot, therefore, be calculated on the results of any one year. *Rhyssa* is intrinsically superior to *Ibalia* and super-parasitism of *Ibalia* by *Rhyssa* is of very frequent occurrence. It is shown that the figures for parasitism by *Ibalia* obtained by the dissection of *Sirex* larvae collected from a number of logs, over a period including summer months, are liable to be very misleading.

Both parasites are very efficient and each may obtain a very high percentage of parasitism, but the combined effects of the two parasites result in a higher percentage of parasitism than when each parasite is working alone.

Parasitism by *Rhyssa* reached its highest when *Sirex* is breeding in material under 3 inches in diameter, as the *Sirex* larvae are then within reach of the ovipositor of *Rhyssa* throughout the whole three seasons of their development. Parasitism by *Rhyssa* is often very low in logs of large diameter because the *Sirex* larvae may be out of reach during the second summer.

Diameter of the material in which *Sirex* is breeding does not affect parasitism by *Ibalia*, but the period of effective activity of the parasite is limited to the egg and early larval stage of the host.

A table is given showing the development of the *Sirex* and parasite complex and indicates what a log may be expected to contain in either summer or winter over a period of four years when one generation of *Sirex* and its parasites is present.

A large tree may support a colony of *Sirex* over a long period of years, and a table is given showing the inter-relationship of *Sirex* and its parasites over a period of seven years, when three generations of *Sirex* are present in the same piece of timber. In such cases, three generations of *Ibalia* and five generations of *Rhyssa* may emerge. A single generation of *Rhyssa* may be the product of one, two, or three generations of *Sirex*. A table is given showing from which generation of *Sirex* each of the generations of *Rhyssa* may arise. A large tree may support a population of more than 3,000 *Sirex* and parasites during that period.

5. Possible factors of control other than parasites are discussed, including birds, fungi, and climatic conditions. It is considered that birds are of little importance under normal conditions. Fungi destroy *Sirex* pupae and adults under certain conditions, but these organisms cause the death of trees and help to increase the amount of suitable breeding material.

Climatic conditions have little effect on mortality and probably do not alter the numerical ratio of host and parasite. Abnormal conditions in the forest tend to result in more favourable breeding facilities for *Sirex*.

6. The economic status of *Sirex* is discussed. The nature of the damage is of a technical character affecting the quality of the timber. For successful oviposition in living trees the limiting factors are rapidity of transpiration and activity of the cambium.

Sirex prefers fresh-felled, perfectly sound timber, and is not dependent on any peculiar pathological condition. Although trees killed by *Fomes annosus* and *Armillaria mellea* are readily attacked by *Sirex* for breeding purposes, that part of the timber actually permeated with the mycelium of these fungi is unsuitable for the insect's development.

It is stated that although *Sirex* is normally of little economic importance in Britain, circumstances may arise when the insect does considerable damage, but this is invariably due to neglect on the part of the owners of the timber concerned. Under normal forest conditions *Sirex* may be considered to be under economic control in Britain, and the parasites *Rhyssa* and *Ibalia* are the chief factors of control. It is pointed out that this view is not shared by all economic entomologists, and an example of adverse criticism of biological control is examined.

7. Reference is made to the present status of *Sirex* in New Zealand, and the presence of *Hylastes ater* is mentioned as an additional factor likely to contribute to the rapid increase of *Sirex*. It is pointed out that although the insects belong to different orders, they form a definite biological association of a particularly dangerous type.

8. Reference is also made to the introduction and establishment of *Rhyssa* in New Zealand. Details of the method of shipment and data showing the condition of the parasites on arrival are reproduced. The reason for the high rate of mortality in some of the shipments is discussed and suggestions are made which it is thought will result in a reduction in mortality and eliminate much loss caused by malformation of the ovipositor, if further shipments are made in the future. The net results of the investigation are summarized.

9. Methods of control are discussed under the headings : (i) Silvicultural and mechanical control ; (ii) biological control.

It is shown that although the first method would bring about the destruction of large numbers of insects, there is no reason to suppose that it would result in the control of *Sirex*. The necessary operations would incur an enormous annual expenditure and for economic reasons cannot be put into practice. On the other hand, it is stated that biological control may reasonably be expected to bring about the desired results if carried out on an adequate scale, and that a comprehensive scheme of biological control could be carried out at relatively little cost.

11. Acknowledgments.

The writer desires to thank the following landowners, His Grace the Duke of Bedford, the Marquess of Bath, the Earl Fortescue and Lord Clinton, also the Forestry Commissioners, for permission to collect the parasites on their estates and for their generosity in gratuitously providing the necessary material. He also wishes to express his indebtedness to their foresters for their kindness in facilitating the work ; to his fellow members of the staff at Farnham House Laboratory for their co-operation in handling the material for shipment, and to Dr. W. R. Thompson, Superintendent of Farnham House Laboratory, Dr. R. Neil Chrystal of the Imperial Forestry Institute, Dr. D. Miller of the Cawthron Institute, New Zealand, Mr. A. F. Clark, Forest Entomologist, State Forest Service, New Zealand, and Dr. J. G. Myers, for the part each has played in contributing to the success of the investigation.

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EXPLANATION OF PLATE 1.

Fig. 1.—*Sirex* larvae, which have escaped parasitism, burrowing in region of pith in winter. (Natural size.)

Fig. 2.—Full-grown *Sirex* larva in pupal chamber in winter. (Natural size.)

Fig. 3.—*Sirex* larval galleries, showing the region in which the larvae have burrowed during the summer while between the two stages shown above. (Natural size.)

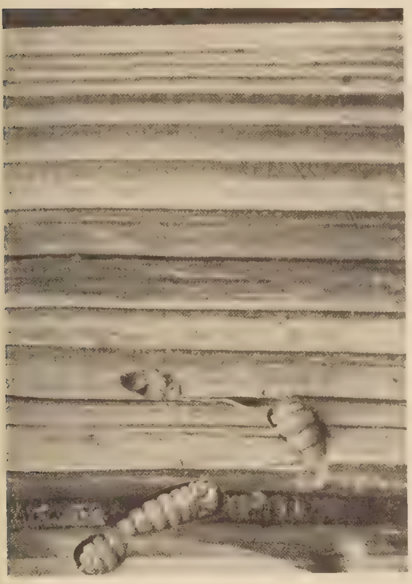
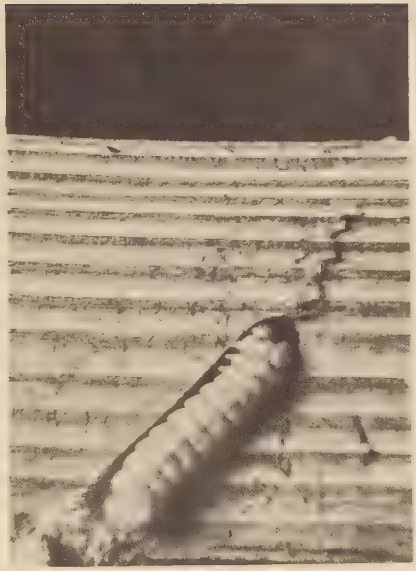


Fig. 1.



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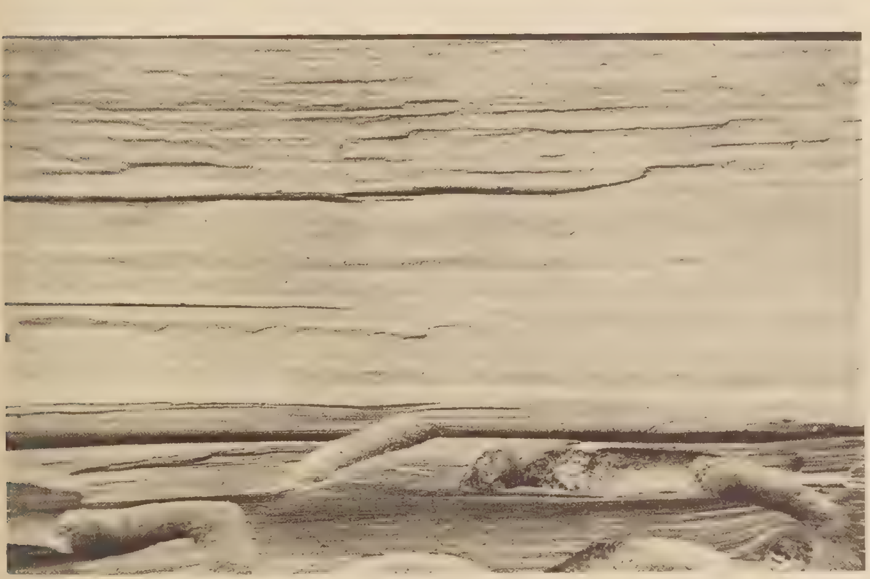

Fig. 3.

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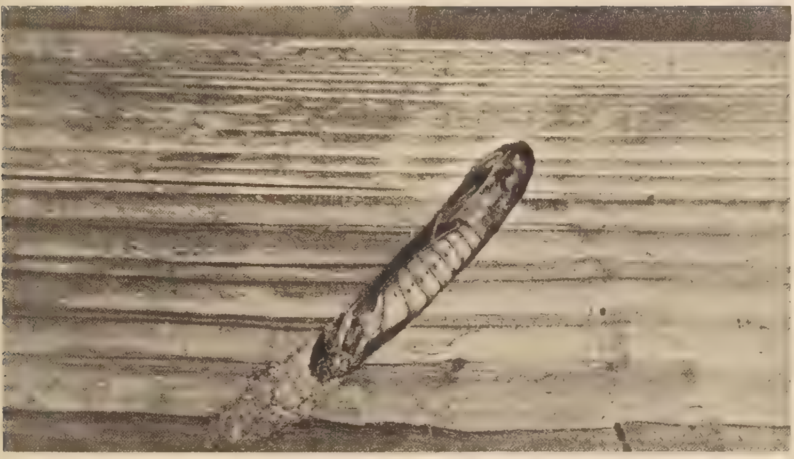
EXPLANATION OF PLATE II.

Fig. 1.—*Sirex cyaneus*, female pupa in pupal chamber.
Fig. 2.—*Sirex gigas*, female adult in pupal chamber ready to emerge.



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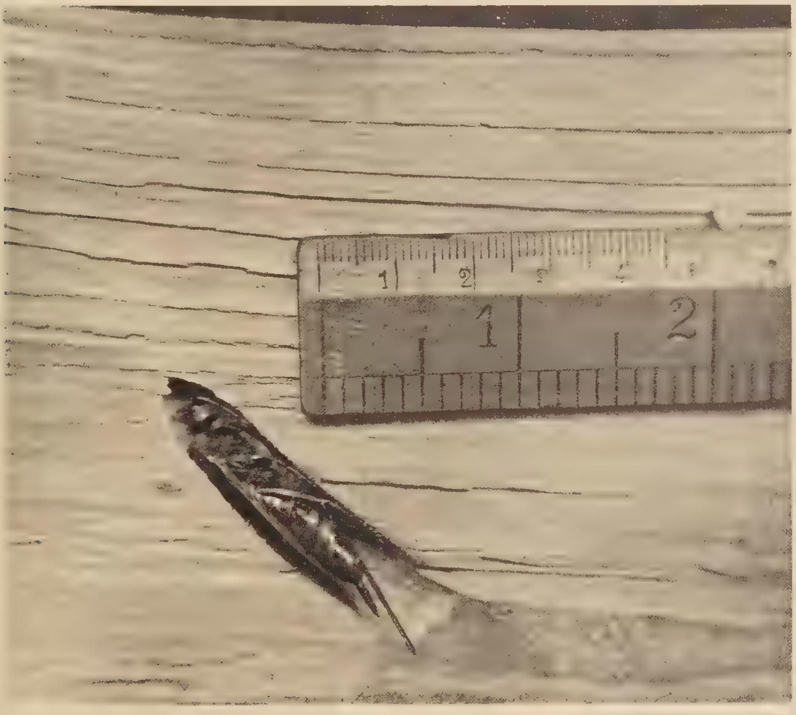


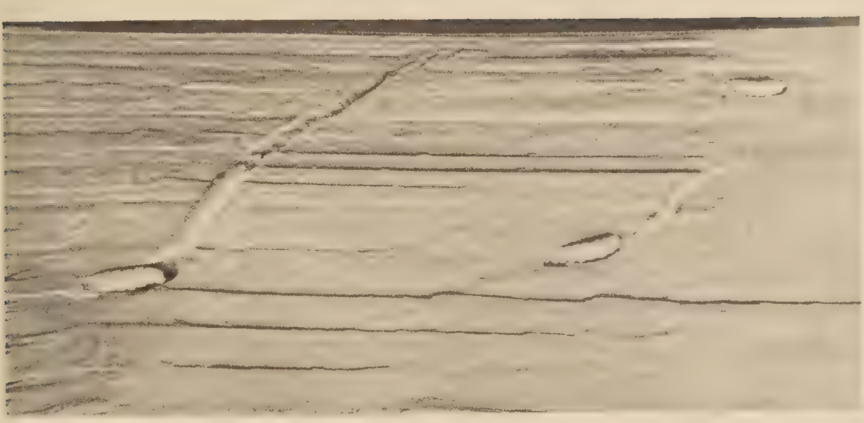
Fig. 2.

Explanation of Plate III.

Fig. 1.—*Rhyssa* larvae, 1st generation ; two are in normal *Sirex* galleries, one is in a gallery characteristic of *Sirex* parasitized by *Ibalia* (super-parasitism). (Natural size.)

Fig. 2.—Full-grown *Ibalia* larvae in pupal chambers, also a *Rhyssa* larva (2nd generation) which has eaten one of the *Ibalia* larvae (hyper-parasitism). (Natural size.)

Fig. 3.—*Rhyssa* larva (2nd generation) in gallery of *Sirex* larva which was nearly full-grown. (Natural size.)



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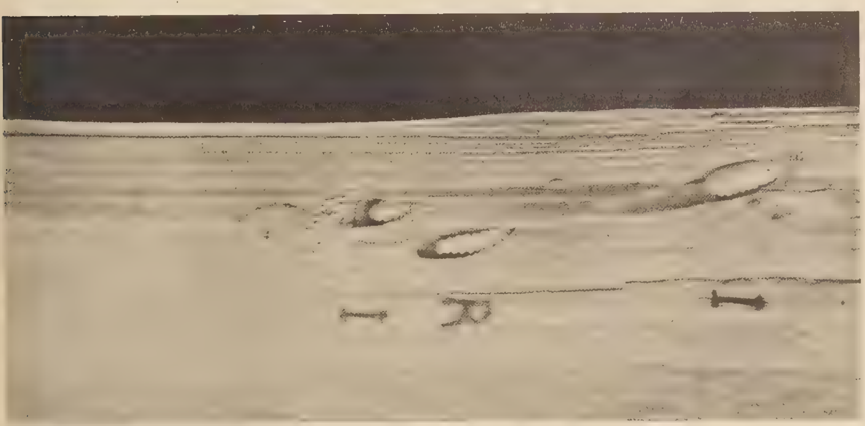

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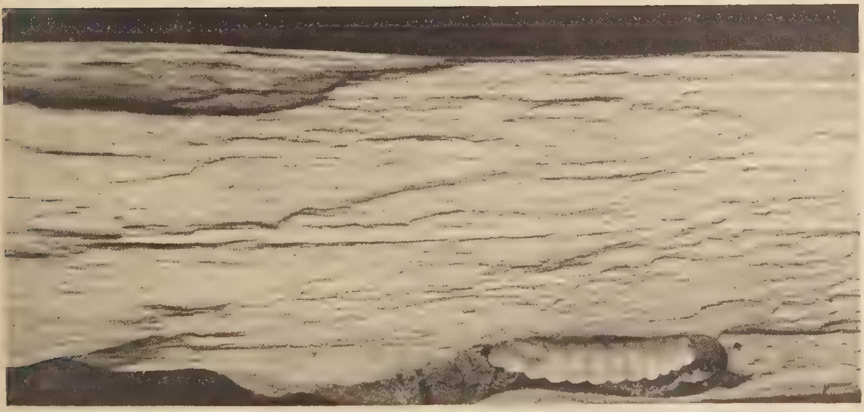

Fig. 3.

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EXPLANATION OF PLATE IV.

Fig. 1.—*Rhyssa* pupa (3rd generation) in pupal chamber of *Sirex gigas*, with remains of full-grown *Sirex* larva.

Fig. 2.—Adult female *Rhyssa* tunnelling exit gallery from pupal chamber of *S. cyaneus*.

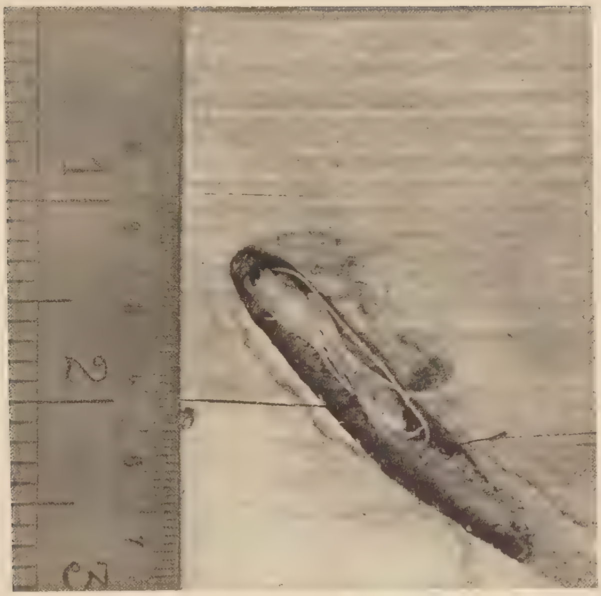

Fig 1.

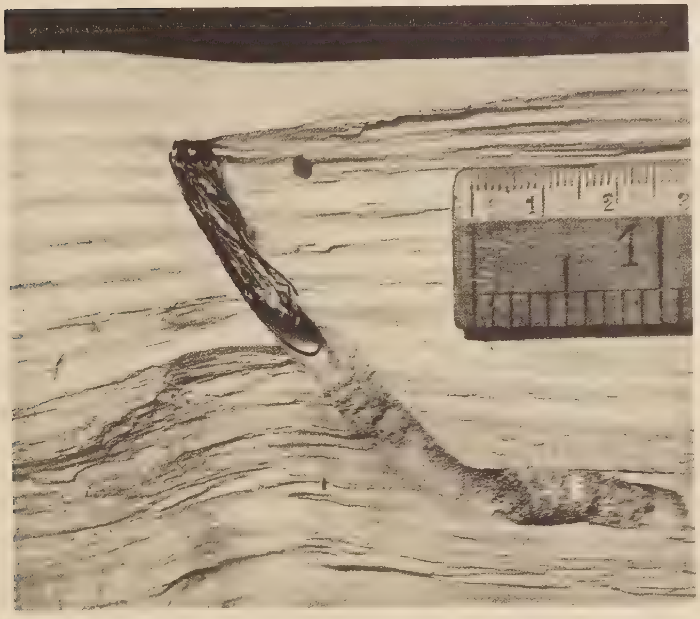

Fig. 2.

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EXPLANATION OF PLATE V.

Fig. 1.—Pupal chamber and exit hole of *Rhyssa* (3rd generation) ; very large specimen. (Natural size.)

Fig. 2.—Sections of silver fir showing exit holes of *Sirex* and parasites.

Fig. 3.—Full-grown larva of *Rhyssa* in pupal chamber of *Sirex* with remains of an adult *Sirex cyaneus*.

PLATE V.

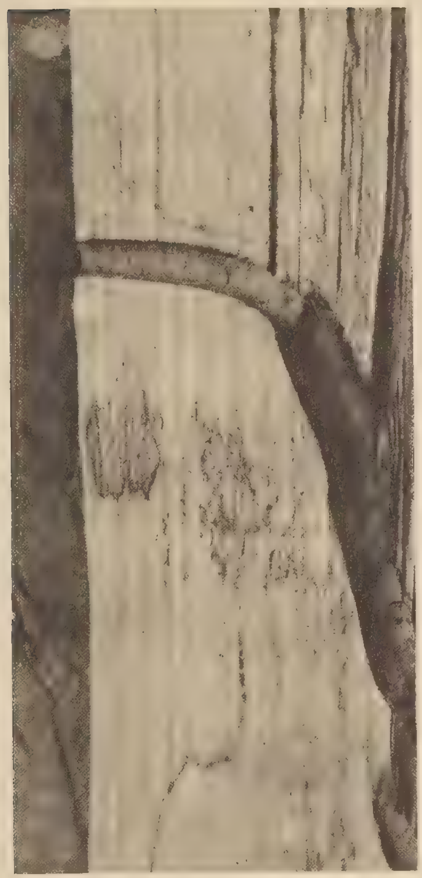
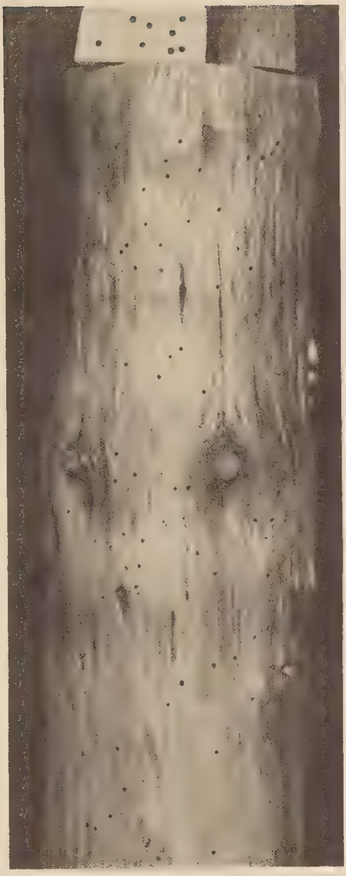


Fig. 1.



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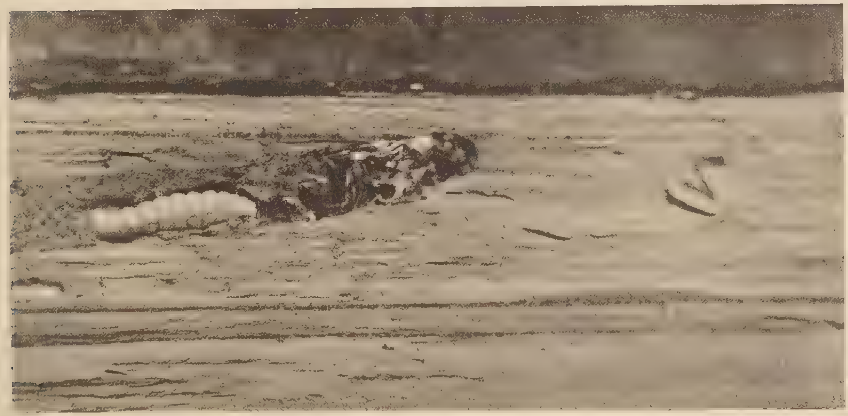

Fig. 3.

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Explanation of Plate VI.

Fig. 1.—Two exit galleries of *Sirex gigas* converging to one exit hole.
Fig. 2.—Adult *Sirex cyaneus* female tunnelling exit gallery. (Natural size.)

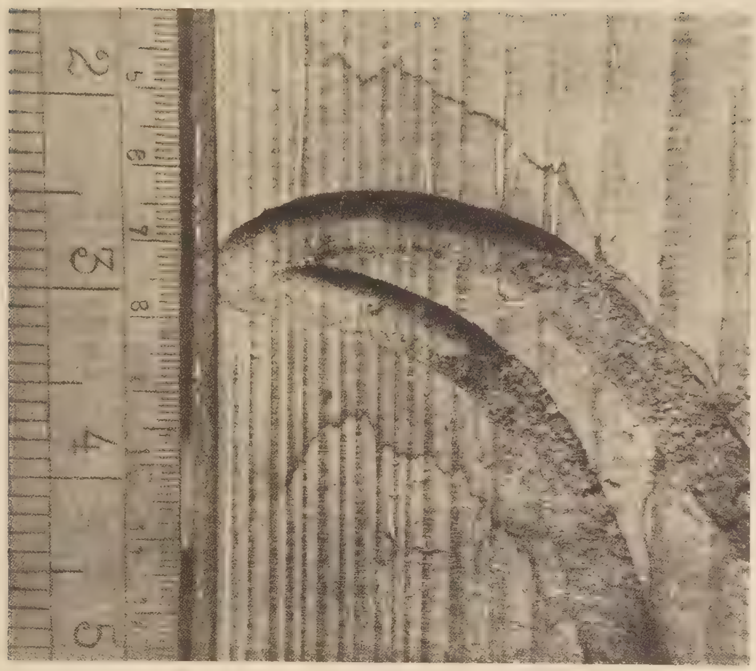

Fig. 1.

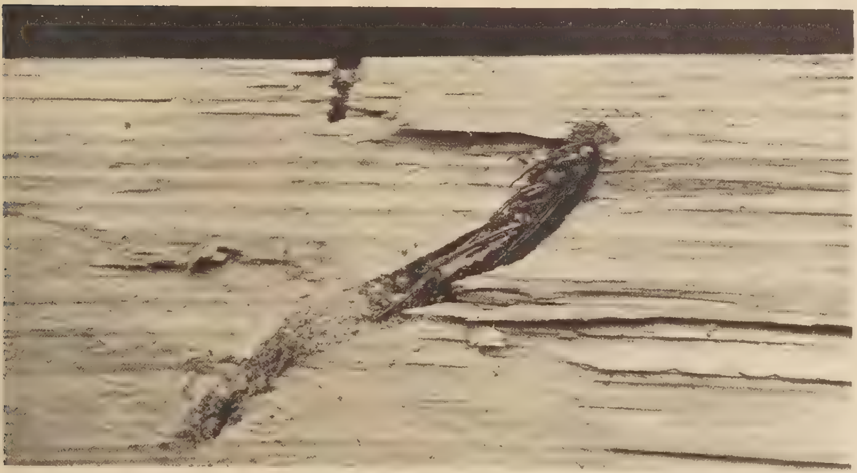

Fig. 2.

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ON TWO SPECIES OF *APANTELES* (HYM. BRAC.) NOT PREVIOUSLY RECOGNISED FROM THE WESTERN PALAEARCTIC REGION.

By D. S. Wilkinson,

Imperial Institute of Entomology.

In this paper I am redescribing and giving some interesting, new, biological information with regard to two species of *Apanteles*, of which one, *A. compressiventris*, has not previously been recorded in the Old World, and the other, *A. plutellae*, not previously recorded from the Western Palaearctic Region ; and I believe that it is better to communicate this information at this time rather than to wait until the completion of the monograph upon which it is known that I am engaged, a matter yet of some years.

I am much indebted to the authorities of the United States National Museum for their continued collaboration with us by exchange of material, for it was by this means I was originally made acquainted with *compressiventris*. It gives me much pleasure, also, to acknowledge my indebtedness to Dr. D. C. Lloyd and Mr. R. L. E. Ford, who so readily undertook the experimental breeding of *plutellae*.

Apanteles compressiventris, Mues.

Apanteles compressiventris, Muesebeck, 1921, Proc. U.S. Nat. Mus., **58,** p. 535.

Apanteles vitripennis, Haliday [*sic*], Reinhard, 1881, Deut. ent. Zeit., **25,** pp. 50–51 (*excl. synn.*).

Apanteles liparidis, Bouché, Lyle, 1925, Ent. Mo. Mag., **61,** p. 123 (*partim*).

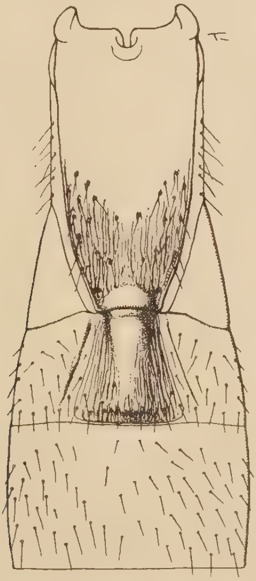

Fig. 1. *Apanteles compressiventris*, Mues., basal tergites, ♀ (×80).

♀♂. Black ; the four front legs entirely (save for the black feet and for commonly some slight but extensive darkening on the tarsi), the trochanters, trochantines, and femora, of the hind legs entirely, the hind tibiae (save for their apical fourth, which is slightly or as commonly strongly darkened), the palpi, tegulae, the venter basally, and the lateral membranous portions of the two, sometimes of the three, basal tergites, red testaceous ; hind tarsi slightly or as commonly strongly darkened, the feet black ; hind coxae basally, sometimes throughout the basal half, or even entirely, black, large areas in the apical half, even the whole of the apical half, and even more extensively still, red testaceous ; tibial spurs pale ; wings quite strongly infumated evenly throughout, and the setae coloured ; wing-veins (save in basal portion of wing), stigma, and metacarp, brown or dark brown ; stigma uniformly opaque.

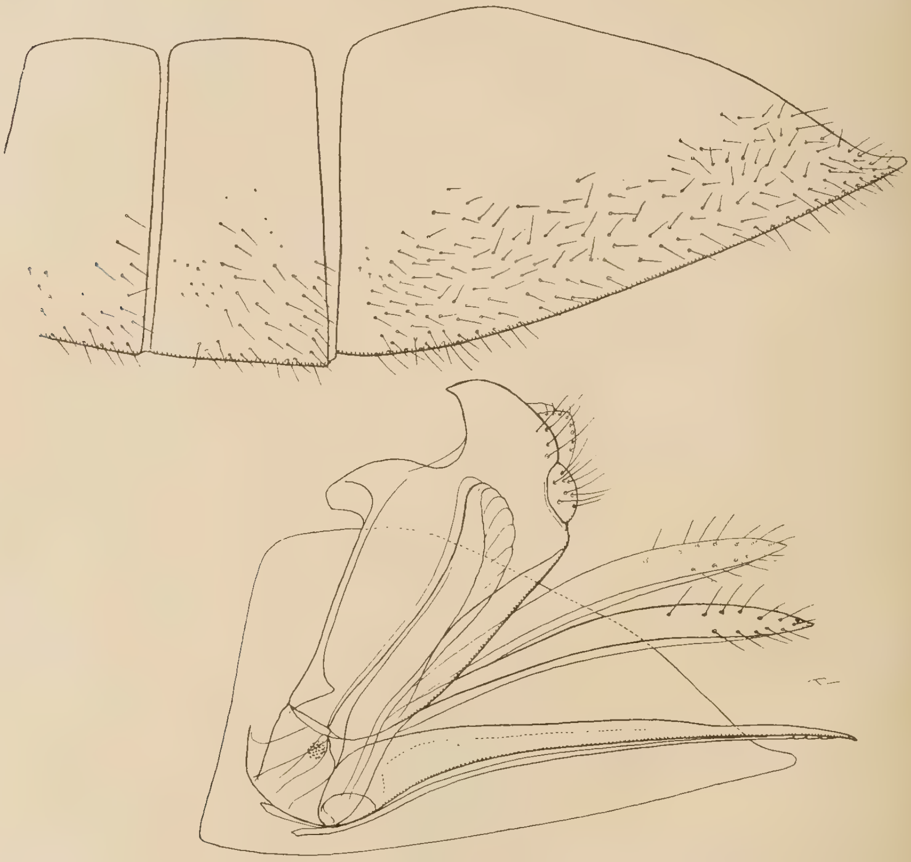

Fig. 2. *Apanteles compressiventris*, Mues., apical ventrites and, below, genitalia, side view, ♀ (×80).

♀♂. *Head* : face, clypeus, frontal orbits, frons, and vertex, minutely punctate (degree 1) ; facial depressions nearer to apex of clypeus than to the eyes ; posterior ocelli equidistant from each other and the eyes ; flagellum of ♀ about equal to or longer than combined length of thorax and abdomen together with twice the length of the head, of ♂ longer than combined length of thorax and abdomen together with three times the length of the head, or longer than three times the length of the thorax.*

---

* In both sexes of the long series of small specimens dated 1935 the flagellum is perhaps a little shorter relatively than as here stated.

Thorax : mesonotum throughout regularly punctate (degrees 2 or 3) ; disc of scutellum minutely punctate ; propodeon in basal half with minute scattered punctures on each side of a median smooth area, which area is commonly more or less wanting, in apical half with minute irregular rugosity, the apical angles with strong rugosities but with large areas entirely smooth and shining, the median apical lunule commonly emitting a very short incipient (or obsolescent) median longitudinal carina. *Wings* : the transverse cubital angled with, and equal to or longer than, the 1st abscissa of the radial, with thickening at their point of junction. *Legs* : hind coxae throughout minutely punctate (degree 2), perhaps rather more sparsely so on outer faces than above ; the hind tibial spurs equal or subequal, half the length of the basal joint of the hind tarsus. *Abdomen* (figs. 1 and 2) : 1st tergite in basal half slightly excavate and entirely smooth, in apical half turned over and with longitudinal aciculation and widely separated minute (degree 3) punctation, the lunule occupying almost the entire apex, but the extreme apical angles depressed ; 2nd tergite all across base smooth and raised to conform with the apex of the 1st, otherwise almost throughout with longitudinal aciculation and much widely separated minute punctation, the sulci not well marked but often lost before reaching apex of tergite ; 3rd tergite throughout with well separated minute punctation, which is often absent in a small triangular median basal area ; succeeding tergites with the usual minute punctation ; ventrites without median longitudinal suture ; ovipositor sheaths shorter than, and the ovipositor equal in length to or rather longer than, the hind femur ; hypopygium large, acute and strongly produced apically.

Length : ♀, 2·25–3·5 mm. ; ♂, 2·0–3·0 mm.

Redescribed from the following material :—BRITISH MUSEUM : Lyle Collection, Eastbourne, a card of eight (7 ♀♀, 1♂), and a card of eight (8 ♀♀), ser. nos. 4710, 4711, 19.v.1924 (*G. T. Lyle*), det. Lyle as *liparidis*, Bouché ; General Accessions, Aberdeen, 2♀♀, 4♂♂, v.1929 (*Graham Smith*). NATURHISTORISCHES MUSEUM, VIENNA : 19 ♀♀, 16 ♂♂ ; 1 ♀, 3 ♂♂ ; 1 ♂ ; a card of four (3 ♀♀, 1♂), Roghf., 1867—all det. Reinhard as *vitripennis*, Curtis ; 12 ♀♀, 1♂, det. Reinhard as *inclusus*, Ratz. ; 3 ♀♀, 1 ♂, 1 ? ; 5♂♂, 1 ?, 1869 (*Reinhard*). K. G. BLAIR'S COLLECTION : a card of eleven (10♀♀, 1 ♂) ; Scilly Is., a card of nine (7 ♀♀, 2 ♂♂), a card of nine (8 ♀♀, 1 ♂), a card of eight (5♀♀, 3♂♂), and a card of thirteen (10 ♀♀, 3 ♂♂), ser. no. 32/11 ; St. Merryn, Cornwall, a card of seven (5 ♀♀, 2 ♂♂), and a card of two (1 ♀, 1 ♂), ser. no. 39/35, all det. Lyle as *fulvipes*, Hal. D. S. WILKINSON'S COLLECTION : England, North Cornwall, 26 ♀♀, 39 ♂♂, June 1935 (*G. V. Bull*), Wilmington, Kent, 8 ♀♀, 6 ♂♂, host coll. iii–iv.1937, par. pup. 6.iv.1937, par. em. 24.iv.1937 (*R. L. E. Ford*).

Further material examined :—BRITISH MUSEUM : Mt. Washington, N. H., 1 ♀, 1 ♂ (*paratypes*). D. S. WILKINSON'S COLLECTION : England, Kent, Gravesend, 79 ♀♀, 11 ♂♂, coll. 10.iii.1938, pup. 18.vi.1938, em. 29.vi.1938. (*R. L. E. Ford*).

Type in the United States National Museum ; cat. no. 22532. *Paratypes* in the British Museum.

Host. Muesebeck originally described this species simply as a parasite of an Arctiid ; and all the material from which I have made the redescription is from an Arctiid host, with the exception of one series where a mistake may well have been made in determining which was the host. From the Arctiid *Phragmatobia fuliginosa*, L., referred to by the recorders under either *Spilosoma* or *Arctia*, is recorded the series from Aberdeen, the series from Vienna dated 1869, the thirty-five females and males, which is doubtless the material referred to by Reinhard under *A. vitripennis*, and the three females, one male and one query also from Vienna, while Blair's series from the Scilly Isles is recorded from either *P. fuliginosa* or *Spilosoma menthastri*, Esp., which is known to us now as *Diacrisia lubricipeda*, L. Dr. Bull's series, Lyle's series determined by him as *liparidis*, Ford's series from Kent and Gravesend, and the card of four from Vienna, are recorded from *Arctia villica*, L. The single male from Vienna is labelled to have been bred from the Nymphalid

Vanessa atalanta, L., but I consider this record is to be treated with very considerable reserve, not only on account of the difference in the family of the host, but also since from the bunch of cocoons attached to the host larva I extracted a further specimen, that proved to be a species of *Microgaster*. The remaining material is without host record.

Cocoons white, held loosely together in a mass. A total of 141 cocoons was observed by us from Ford's single larva of *A. villica* from Gravesend.

Commentary. Muesebeck originally described this species from " many specimens of both sexes," from Mount Washington, New Hampshire, U.S.A., and as a parasite of an Arctiid. In the British Museum are a female and a male labelled as *compressiventris* in Muesebeck's own handwriting, with the correct United States Museum catalogue number on a paratype label, and with the biological information exactly as stated in the original description ; they were received in 1930 by the British Museum from the United States National Museum, in exchange. These two specimens are, obviously, to be accepted as authentic material, and they agree perfectly and in the minutest detail with all the other material from which I have made the redescription, save only in that their anterior coxae are rather more darkened and the flagellum apparently rather shorter.

In my key (1932, Trans. Ent. Soc. London, **80,** and as subsequently emended, especially in 1934, Stylops, **3,** p. 146) I must run this species on both sides of couplet 12, since the coloration of the hind coxae is so variable. From the first part of this couplet *compressiventris* runs to couplet 14a, which should be altered as follows :—

14a. Hypopygium acute and strongly produced apically ; N. America, Europe *compressiventris*, Mues.
Hypopygium not so describable..14a/1
14a/1. *as existing* 14*a*.

Couplet 41 is to be deleted, and the second part of couplet 40 altered to lead to couplet 42 ; and then, from the second part of couplet 12, *compressiventris* will run easily to couplet 44, which should be altered as follows :—

44. Hypopygium acute..44a
Hypopygium truncate..45

44a. Hypopygium somewhat acute, not produced apically ; 1st abscissa of radial longer than transverse cubital ; stigma shorter than metacarp ; Palaearctic, Nearctic..*porthetriae*, Mues.
Hypopygium acute and strongly produced apically ; transverse cubital equal to or longer than 1st abscissa of radial ; stigma and metacarp of equal length ; Palaearctic, Nearctic ....*compressiventris*, Mues.

Apanteles plutellae, Kurdj.

Apanteles plutellae, Kurdjumov, 1912, Rev. Russe d'Entom., **12,** pp. 226-227.

Apanteles ruficrus, Haliday, Bignell, 1901, Trans. Devon. Assoc. Adv. Sci., **33,** p. 669 (*partim*).

♀. Black ; trochanters to some small extent or even wholly, trochantines, femora, tibiae, and tarsi, of the four anterior legs (save for the darkened feet, and slightly darkened tarsi and apex of middle tibiae), the four anterior coxae occasionally at extreme apex, hind trochantines, hind femora more usually with the extreme base and about the basal half below, but always with at least the basal half below and commonly with the whole of the basal half or even still more extensively, hind tibiae (save for apex or apical fourth), tegulae, tibial spurs and palpi more or less, and basal ventrites, red testaceous ; 3rd tergite often laterally or in lateral thirds, sometimes throughout the lateral thirds, occasionally only narrowly across extreme apex, and occasionally entirely, red testaceous ; wings infumated, and the setae coloured ; costal veins in basal half and other veins at base of wing testaceous ; costal veins otherwise, remaining veins, stigma, and metacarp, brown ; stigma uniformly opaque.

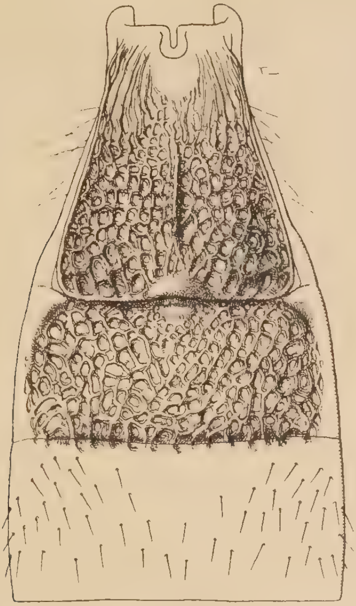

Fig. 3.—*Apanteles plutellae*, Kurdj., basal tergites, ♀ (×80).

♂. Agrees closely with above colour description of ♀ save that in many examples the legs are much darker, so that the four anterior femora are often considerably darkened, the hind tibiae often black in the apical two-fifths or half, and the hind femora extensively or even wholly black ; the red testaceous colouring on the 3rd tergite would appear to occur rather less frequently than in ♀.

♀♂. *Head* : face throughout and frontal orbits closely punctate (degree 3) ; facial depressions clearly nearer to apex of clypeus than to the eyes ; frons and vertex punctate (degree 2) ; posterior ocelli about equidistant from each other and the eyes ; flagellum of ♀ longer than combined length of head, thorax, and abdomen, but shorter than combined length of thorax and abdomen together with twice the length of the head, of ♂ about equal to or rather shorter than combined length of thorax and abdomen together with three times the length of the head, or about equal to three times the length of the thorax. *Thorax* : mesonotum along the lines of the notauli, narrowly down a medial longitudinal line, and in a large area into which these converge and which occupies at least half of the posterior half of the mesonotum, the anterior margin and the lateral margins, rugoso-punctate and dull, otherwise shining and punctate (degree 3), narrowly across posterior margin shining and entirely smooth ; scutellar sulcus strongly crenulate ; disc of scutellum throughout rugoso-punctate, or at least strongly punctate (degree 4) ; propodeon very strongly and very coarsely reticulately rugose, slightly sunken in the median longitudinal area, and occasionally with a median longitudinal carina somewhat evident. *Wings* : 1st abscissa of radial angled with, and about equal in length to, the transverse cubital, the upper portion of the basal vein short, and the metacarp equal in length to the stigma. *Legs* : hind coxae rugose ; hind tibial spurs equal in length, half the length of the basal segment of the hind tarsus. *Abdomen* (figs. 3 and 4) : 1st tergite at base strongly excavated, medianly quite strongly (even very strongly) tumescent and sometimes with some sort of short median longitudinal carina, apically turned over, in the excavated basal portion more or less smooth, otherwise rugoso-punctate; 2nd tergite rugose; 3rd tergite smooth broadly across apex, narrowly across base, and in a large median basal triangular area, otherwise minutely punctate, this punctation rather variable in extent and density, apparently more extensive and more densely placed in ♂ than in ♀; succeeding tergites with the usual minute punctation; ventrites without median longitudinal suture; ovipositor sheaths rather shorter than the basal segment, about equal to the combined length of the 2nd and 3rd segments, the ovipositor rather longer than the basal segment, shorter than combined length of basal and second segment, of the hind tarsus; hypopygium with its apex cut away to form a lower-posterior margin.

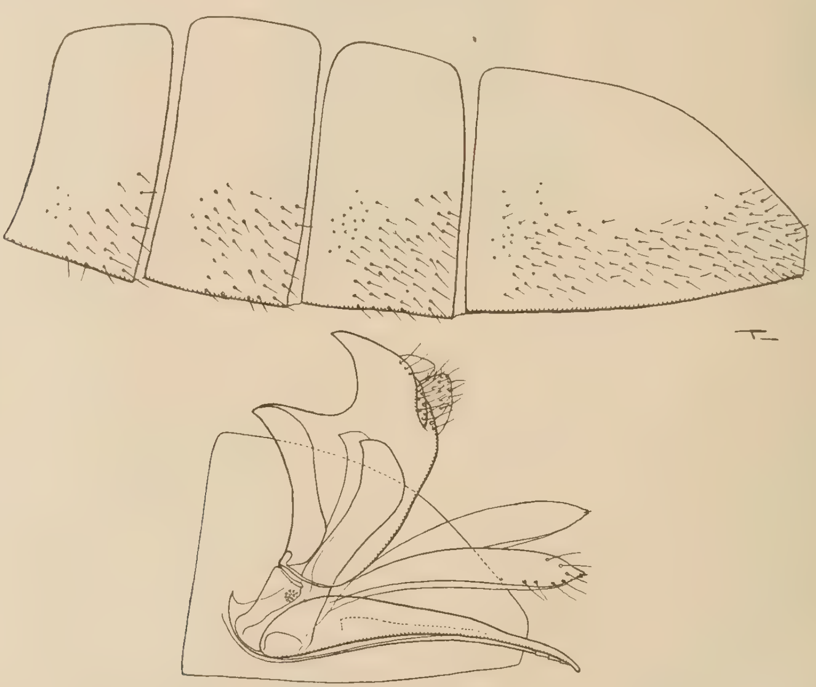

Fig. 4. *Apanteles plutellae*, Kurdj., apical ventrites and, below, genitalia, side view, ♀ (× 80).

Length, 2·0–3·0 mm.

Redescribed from the following material:—BRITISH MUSEUM: Marshall Collection: 1 ♀, "N," 1.ix.1884, 1 ♂, "N," in coll. under *ruficrus*. PLYMOUTH MUSEUM: Bignell Collection: a card of two (2 ♀♀), Crabtree, Sept. 2nd, Bign. reg. nos. 1 and 2, in reg. dated 10.ix.1880 and det. as *glomeratus*, in coll. under *ruficrus*; 1 ♀, Bign. reg. no. 1916, in reg. dated 1.viii.1884 and recorded from Oreston Quarry, 2 ♀♀, Bign. reg. nos. 2038, 2079, in reg. dated 21.viii.1884 and 9.ix.1884 and recorded from Bickleigh, 2 ♀♀, Bign. reg. no. 2116, in reg. dated 28.viii.1884 and recorded from Crabtree, 1 ♀, Bign. reg. no. 2851, in reg. dated 13.vii.1885, all det. as *ruficrus*. NORWICH CASTLE MUSEUM: Bridgman Collection: 3 ♀♀, Bridg. reg. no. 762, in reg. dated "Bignell 1885" and det. as *ruficrus*, a card of four (3 ♀♀, 1 ♂), 2.vii.1887—all in coll. under *ruficrus*. MUSEO CIVICO DI GENOVA: Cyrenaica, R. U. Agrario, Bengasi, 7 ♀♀, 18261.I.31, 18264–18269.I.31 (*Geo. C. Krüger*), Bengasi, 1 ♂, iii.1916

(*V. Zanon*). IMPERIAL INSTITUTE OF ENTOMOLOGY : Italy, Lodi, 1 ♀, I 6, vii.1938, Sarzana, 2 ♀♀, 2 ♂♂, I 2, vii.1938, Rogoredo, 1 ♀, 2 ♂♂, I 7, vii.1938, France, Grenoble, 2 ♂♂, F 4b, vii.1938 (*J. Muggeridge*) ; Hoorn, Holland, 16 ♀♀, 15 ♂♂, ix.1937, and 5 ♀♀, 7 ♂♂, i.x.1937, 3 ♀♀, 7 ♂♂, *undated* ; Farnham House Laboratory, 15 ♀♀, 20 ♂♂, pup. 4.x.1937, em. 24.x.1937 ; India, United Provinces, Dehra Dun, 2 ♀♀, nos. 3169, 3170, 17.iv.1934 (*S. N. Chatterjee*) ; Morocco, Rabat, 3 ♀♀, 4 ♂♂ (*Bremond*), Marrakech, 13 ♀♀, 8 ♂♂, no. 1005, i.1936 (*Perret*), Oujda, 2 ♀♀, 2 ♂♂, no. 305, 30.i.1937 (*Vidal, per P. Regnier*), Parc Lyautey, 1 ♀, no. 436/413e, 9.i.1930 (*Bouhelier*) ; Old Bolingbroke, Spilsby, Lincolnshire, 1 ♀, 1 ♂, 1.vii.1935 (*M. W. Graham*). D. S. WILKINSON'S COLLECTION : British Isles, 3 ♀♀, 2 ♂♂, 1936 (*Dr. G. V. Bull*) ; England, Essex, Benfleet, 1 ♀, 1936 (*S. Wakely*) ; England, Kent, Folkestone, 1 ♀, 2 ♂♂, 22.viii.1935, Wrotham, 1 ♀, i.vii.1935, Funton, Salt Marshes, 1 ♀, 5 ♂♂, coll. 28.vi.1937, em. 30.vi.1937, Slades Green, 7 ♀♀, 3♂♂, pup. 19.viii.1937, em. 30.viii.1937, Bexley, 3♂♂, coll. 28.v.1938, em. 13.vi.1938, Gravesend, 3 ♀♀, 3 ♂♂, Gravesend, 1 ♀, 1 ♂, pair A, 1 ♀, 1 ♂, pair B, 1 ♀, 1 ♂, pair C, 3 ♀♀, 4 ♂♂, pairs D, vi.1938, Surrey, Dunsfold, 10 ♀♀, 1 ♂, 15.vii.1936, Cambridge, Gog & Magog Hills, 2 ♀♀, 26.viii.1937 (*R. L. E. Ford*), Hampshire, Southampton, 1 ♀, coll. 1.vi.1938, em. 20.vi.1938 (*L. T. Ford*) ; Farnham House, 3 ♀♀, 3 ♂♂, offspring of pair A, 3 ♀♀, 3 ♂♂, offspring of pair B, 3 ♀♀, 3 ♂♂, offspring of pair C, 9 ♀♀, 6 ♂♂, offspring of pairs D ; England, E. Sussex, Staplecross, 17 ♀♀, 8 ♂♂, vi.1936 (*D. S. Wilkinson & P. E. Ward*), Surrey, Chiddingfold, 2 ♀♀, 1 ♂, vi.1936 (*D. S. Wilkinson & B. O. Petrides*).

Type believed to be lost.

Host. Kurdjumov originally described *A. plutellae* as a parasite of the Tineid *Plutella maculipennis*, Curt., and, of the material from which I have now redescribed the species, the three series from Holland, the two females from India, the thirty-five females and males from Farnham House dated 1937, and the offspring of the pairs, A, B, C, and D, were bred from this host. Of the remainder of the material before me, Ford's series from Folkestone, Dunsfold, Slades Green, Bexley, and Gravesend, are recorded from the Nymphalid *Vanessa*, now *Aglais*, *urticae*, L., and the two series from Staplecross and Chiddingfold from a species of *Aglais*, probably *urticae*, L. Bignell's females numbered 1 and 2 are recorded by him in his register to have been bred, respectively, from the Pierids *Pieris rapae*, L., and *P. brassicae*, L., and Ford's series from Wrotham from the Pierid *Euchloë cardamines*, L. Bignell's single female number 2851 is recorded from a small larva of the Agrotid *Cucullia chamomillae*, Schiff., Dr. Bull's series from the Arctiid *Arctia*, now *Diacrisia*, *urticae*, Esp., Ford's series from Funton from the Lasiocampid *Malacosoma castrensis*, L., Perret's series from the Lymantriid *Ocnogyna baetica*, Ramb. subsp. *meridionalis*, Seitz, and Krüger's seven females from a species of the Lymantriid genus *Orgyia* very near to *antiqua*, L., Bremond's and also Bouhelier's material from the Notodontid *Thaumetopoea herculeana*, Ramb., and Wakely's and also L. T. Ford's single female from the Pterophorid *Agdistis bennetii*, Curt. Finally, Bridgman's cardful of four is recorded " from *verbasci*," by which undoubtedly is meant the Agrotid *Cucullia verbasci*, L., as referred to as a host by Bignell (1901, p. 669), and Muggeridge's material from France and Italy is recorded in each case simply from a cocoon found on cabbage, Zanon's single male is labelled " on broad beans," and Ford's Cambridge material was only swept. The remainder of the material is without host record.

In the literature there are only a few records of *A. plutellae*, namely those of Reichardt (1919), Meyer (1926, 1927), and Tzedeler (1931), who all refer to the species as a parasite of *Plutella maculipennis*, and that of Bignell (1901, p. 669), who, under *Apanteles ruficrus*, gives as hosts the Agrotids *Cucullia verbasci*, L., and *C. chamomillae*, Schiff., to which records I have referred above.

The specimens from Gravesend bred by Ford from *Aglais urticae* are of considerable interest since with this material we succeeded in proving what I had long been certain was the case, namely that the *Apanteles* bred from *Plutella maculipennis* and

Aglais urticae were the same species. Ford sent to Farnham House the cocoons he had obtained at Gravesend, and, by arrangement with Dr. Thompson, these were received and dealt with by Dr. D. C. Lloyd. Lloyd, with whom we had previously discussed the problem and to whom I am very much indebted for the trouble he has taken over the matter, subsequently wrote me, on my request, a short report on the procedure he adopted for this experiment ; and I give this report here :—" The twenty-eight cocoons ex *Aglais urticae*, which were forwarded in the first half of June, 1938, were capsuled on receipt, and on emergence 3 pairs, A, B, and C, were selected and left for 12 hours in small tubes for feeding and copulation. Each pair was then confined in muslin-topped cylinders, inside which was placed a small glass pot containing a few small kale leaves ; and approximately fifty second and third instar larvae of *Plutella maculipennis*, Curt., were placed on each plant. These larvae of *P. maculipennis* were quite free from parasites as they were obtained from a stock which has been bred continuously in the laboratory for the last three years. The *Apanteles* readily attacked these larvae, and during the succeeding three weeks several hundred parasitic cocoons were collected from the plants, the host larvae and cabbage having been renewed every five days. A similar result was obtained when ten individuals of unknown sex were confined with this host. It therefore appears quite definite that *Apanteles plutellae*, Kurdj., is able to utilise both *P. maculipennis* and *A. urticae* as a host."

For the purposes of study and comparison I mounted only a few of the offspring of each of these parents, as I have previously shown. The exact numbers bred from each parent are, I think, not without interest, and are as follows :—Parents A produced 33 ♀♀, 19 ♂♂, and 99 unhatched, a total of 151 ; parents B, 23 ♀♀, 17 ♂♂, 101 unhatched, a total of 141 ; parents C, 16 ♀♀, 12 ♂♂, 47 unhatched, a total of 75 ; and parents D, 50 ♀♀, 26 ♂♂, 175 unhatched, a total of 253.

In conclusion, it should be stated that *Apanteles plutellae* is a solitary parasite.

Cocoons pale cream, solitary.

Commentary. Kurdjumov originally described his *plutellae* from five females and one male reared in 1910 at the Experimental Station, Poltava, as a parasite of *Plutella maculipennis.* This original material, together with the type—if a type ever existed, which Dr. B. P. Uvarov, who knew Kurdjumov, thinks unlikely—is probably lost. It is abundantly clear, nevertheless, both from Kurdjumov's original description, which was excellent, and from the host, that I have in fact Kurdjumov's species before me. The original description agrees perfectly with all my material, save only in the length of the male antenna, Kurdjumov's single male doubtless having its antennae damaged since they were described as shorter than those of the female.

In my key (1932, Trans. Ent. Soc. London, **80,** and as subsequently emended, especially in 1937, P. R. Ent. Soc. London, **6,** B, p. 69) this species runs easily to *ruficrus*, Hal., in couplet 71a. It is, indeed, remarkably close to *ruficrus*, but is nevertheless always easily distinguished by the characters I give below. Couplet 71a should be altered as follows :—

71a. Tegulae red testaceous 71a/1
Tegulae black 71b

71a/1. Four anterior coxae entirely red testaceous ; 3rd tergite with a single transverse row of, and occasionally some few other, minute punctures ; cocoons white, more usually gregariously placed ; cosmopolitan .... *ruficrus*, Hal.

Four anterior coxae almost invariably entirely black ; 3rd tergite invariably with much minute punctation ; cocoons pale cream, solitary ; Palaearctic *plutellae*, Kurdj.

THE AMAZON FLY (*METAGONISTYLUM MINENSE*, TOWNS.) IN BRITISH GUIANA.

By L. D. Cleare,

*Entomologist, Department of Agriculture, British Guiana.**

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1. History of the Project.

In 1932 on an expedition in Brazil, Dr. J. G. Myers, of the Imperial Institute of Entomology, while in search for suitable parasites for introduction into this and other colonies in the West Indian area, discovered the Tachinid fly *Metagonistylum minense*, Towns., known generally now as the Amazon fly, as an important parasite of *Diatraea saccharalis*, F., in the vicinity of Santarem on the Amazon, and as the result of his investigations there, formed the opinion that it would be a suitable parasite for introduction into British Guiana.

On his return to British Guiana in January 1933, Dr. Myers acquainted the Sugar Producers' Association of this Colony of his discovery, and suggested the utilization of the parasite in the cane-fields of British Guiana. The Association undertook to bear the cost of the introduction of the parasite and provided a sum of £2,000 for this, the fund being administered by the Director of Agriculture.

In May 1933, Dr. Myers, accompanied by Mr. A. H. Pickles, Entomologist of the Sugar Investigations Committee of Trinidad, and Mr. L. C. Scaramuzza of Cuba, left Georgetown for the Amazon district by way of the hinterland of British Guiana for the purpose of making collections of the parasite for shipment to this country. The first shipment of the parasite arrived in British Guiana on 30th August, 1933.

An account of the discovery of the fly, the return journey to Brazil and the collection and shipment of the insect from Brazil to British Guiana, has been published already by Myers (11).

The present account deals, therefore, only with such of the work as was undertaken in British Guiana either by the writer personally or directly under his control, namely, the receiving of the parasite in this country and the rearing of the flies from the initial shipments, the subsequent rearing of large numbers of flies for the colonization of the sugar-estates of the Colony, including the training of East Indian laboratory assistants for work on the sugar-estates and the supervision of the rearing work on the estates. This work extended over a period of twenty months, from September 1933 to April 1935. Since then, the writer has been closely associated with the Amazon fly situation in the Colony and during the past year (1937) was engaged on a status survey of the fly in British Guiana. In conjunction with Myers' paper the present account should form a more or less complete record of the introduction and establishment of this insect in British Guiana.

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* Seconded as Entomologist-in-charge, Sugar-cane Moth-borer Investigations, Colonial Development Fund, July 1931 to April 1935.

The introduction of the Amazon fly into British Guiana was the first importation of this insect into any country and its first use in biological control. Since then the Amazon fly has been introduced into the islands of St. Lucia, Trinidad and Puerto Rico from material bred in British Guiana, and into the island of Antigua from St. Lucia. These introductions do not come strictly within the scope of this paper so will merely be touched upon in another section.

2. Introduction of the Parasite.

Shipments received.—The collection and transport of the insect to British Guiana has been dealt with fully by Myers (11) and need not be repeated here.

The first trial consignment of puparia was received in Georgetown by registered air mail (Pan-American Airways) on 30th August, 1933. Of the 57 puparia sent on that occasion, flies had emerged from 31 *en route* and the insects were already dead when the package was received, and from the remaining 26 puparia only three flies were secured and a fourth died during emergence. The air mail on this occasion was 23 hours late on its schedule in arriving at Georgetown, and this, no doubt, to some extent accounted for the high mortality of this consignment. The later consignments showed considerable improvement as regards the percentage of flies secured.

From a total of 3,000 puparia shipped from Brazil, 1,409 flies, or 46·9 per cent., were secured in British Guiana ; 935 puparia (31·2 per cent.) failed to produce flies, while 592 flies (19·7 per cent.) emerged and died in transit, and 64 puparia (2·1 per cent.) produced secondary parasites ; making a total of 1,591 or 53·1 per cent. "failures."

Considering the long voyage, the difficulties of transport, and the narrow margin which the pupal period of the insect allowed to accomplish it, the number of flies secured must be considered good.

Receiving and handling the material.—The packages containing the puparia after coming down the Amazon in a special launch were posted by registered air mail at Para. The arrival of the launch at Para was made to synchronise with the departure of the Pan-American Airways plane which runs a regular weekly service between that port and Miami, Florida, U.S.A., via French, Dutch, and British Guiana and certain West Indian islands, and in this way a minimum of delay was obtained.

The time of approximate arrival of the plane at Georgetown being previously ascertained, the writer took charge of the packages personally at the General Post Office, Georgetown, as soon as the mail was received there, and conveyed them immediately to the laboratory.

The puparia in the earlier shipments were packed in damp fibre, but later when bagasse* that was sent from British Guiana was available, in that material, in 2 oz. ointment tins, the number of puparia in each tin varying somewhat according to the total number in the shipment, the maximum being about fifty in any one tin. The ointment tins were then packed in a liberal amount of cottonwool in a cardboard box and the whole wrapped.

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* Sugar-cane after the juice has been extracted. With modern manufacturing methods it is reduced to a fine sawdust-like form.

As the journey down the Amazon from Santarem to Para occupied some six days by launch, and the plane trip from Para to Georgetown a further day and a half, and as the puparia had to be collected some days before, it was natural that there should have been a fairly high percentage of adults emerging *en route*. The majority of such flies died before the receipt of the packages and constitute 37·2 per cent. of the total failures. Some of these flies, probably those which emerged only a few hours before the actual receipt of the packages at Georgetown, were always found crawling about in the tins when they were opened and it was possible to save a number of these.

On arrival in the laboratory the packages were opened within a special glass-sided cage in order to secure any secondary parasites that might have emerged in transit, and the newly emerged flies which were found to be still alive were collected and transferred to suitable cages. The puparia were then sorted and those from which flies had emerged removed, the remainder being transferred, five at a time, to cylindrical glass lamp-chimneys of 2½ inches diameter, one end standing in damp sand and the other being plugged with cotton-wool. In these the flies subsequently emerged and were transferred thence to cages.

From the earlier consignments some of the flies were released within a day or two of emergence, and some retained for rearing trials in the laboratory.

Secondary parasitism.—In spite of the care exercised at the sending end, as was to be expected, a small number of the puparia received produced secondary parasites. Of the 3,000 puparia received in shipments, 64, or 2·1 per cent., produced such secondary parasites. Three secondary parasites were thus secured, namely, *Melittobia* sp. (EULOPHIDAE), *Trichopria* (*Ceratopria*) sp. (DIAPRIIDAE), and *Signophora dipterophaga*, Girault (ENCYRTIDAE), the last of which, already known as a secondary parasite of *Leskiopalpus* (*Stomatodexia*) *diadema*, Wied., in British Guiana, being predominant.

3. Bionomics.

The fly *Metagonistylum minense* was first described by Townsend (19) in 1927. Subsequently it was redescribed by Aldrich (1). In 1933 Monte (10) recorded it as attacking *Diatraea saccharalis*.

The only country in which the insect is known to occur naturally at present is Brazil. In that country, however, its range is considerable. First recorded from the Lower Amazon district, it has been discovered recently by Harland (9) in the vicinity of São Paulo. Harland suggests that the insect in the São Paulo area is a distinct biological race.

The adult of *Metagonistylum minense* is an insect of striking and characteristic appearance, and even in a general way is not likely to be mistaken for other flies parasitic on *Diatraea*, the large and prominent antennae, carried extended in front of the head, serving readily to distinguish it in the field.

The fly varies considerably in size, and may measure from 6·5 mm. to 10·0 mm. long, and is about 3½ to 4 times as long as it is broad. The antennae are black in colour, large and prominent, and protrude in front of the head ; the front of the head is considerably produced and cone-shaped ; the thorax is bluish-grey with two darker longitudinal stripes ; the abdomen reddish-brown with a median darker stripe, showing bluish-grey reflections in certain lights, the last segment being much darker, and there are many strong bristles ; the wings are large and strong and of a smoky brown colour, the legs are black. There is no difference in size between the sexes, but they may be usually distinguished superficially by the shape of the abdomen, the male abdomen being rather more blunt and more bristled than that of the female.

The newly emerged larvae are small, measuring only 0·6 mm., and very active. When they become fully grown they may measure from 12·1 mm. to 13·9 mm. in length.

The puparium when first formed is chestnut-brown, but becomes darker later as development proceeds; it is oval in shape, both ends being evenly rounded, and may vary from 5·4 mm. to 8·8 mm. long and from 2·2 mm. to 3·1 mm. broad, depending upon the food available for the larva. It may be readily distinguished from the puparium of the other fly parasites of *Diatraea* by means of the anal spiracles.

Life-history.—Myers (12) has given a short account of the life-history and bionomics of the fly, based partly on rearings on the Amazon and partly on the work in British Guiana. During the course of the very extensive laboratory rearings which were carried out in British Guiana the writer was able to obtain considerable data on the life-history and bionomics of the insect and these will now be given.

The total life-cycle of the insect varies from 10 to 27 days, of which 5 to 9 days are spent as a larva within the host and 7 to 9 days in the puparium. Laboratory rearings of 20,556 individuals gave a mean life-cycle of 16·77 days.

Of 20,556 flies, 6,132 (29·8 per cent.) had a total life-cycle of 16 days, in 26·8 per cent. it was 17 days; in 15·0 per cent. it was 18 days; in 13·3 per cent. it was 15 days; and in 6·3 per cent. it was 19 days. So that for 91·2 per cent. of the flies the life-cycle was between 15 and 19 days. The life-cycle varied from 10 days (0·39 per cent.=8 flies) to 27 days (0·001 per cent.=1 fly).

The adult female deposits eggs which hatch immediately on deposition, the empty egg-shell being at times plainly visible to the naked eye, and two or three larvae are so released at a time. Deposition takes place either at the entrance of the *Diatraea* tunnel or on the cane-stalk in the vicinity of tunnels, and the young larvae may wander about considerably before finding a host, while doubtless a very large proportion never do encounter a *Diatraea* larva and consequently perish. One or more larvae may also enter a single host larva.

When fully developed the larva leaves the host, which has by that time died and putrefaction set in, and pupation occurs either within the *Diatraea* tunnel, behind a broad leaf-sheath of the cane, or the larva may fall to the ground where pupation takes place. From five to twelve days is spent in the puparium, after which the adult fly emerges.

Mating.—Mating occurs from a couple hours after the emergence of the fly from the puparium to as long as six or more days after this. It takes place with the insects in the resting position, quite often with the head downwards, but the body of the female is rather closely appressed to the surface on which she rests. The body of the male is generally in the same axis as that of the female, the forepart being raised somewhat on its forelegs and the abdomen depressed so as to make contact with the female. During coition the male sometimes makes violent convulsive and apparently excited movements as if to secure better connexion. The genitalia of the male are visible during coition.

Mating commences at times with a short struggle, but at other times takes place quietly, the male merely approaching the female and getting into position. There appears, however, usually to be a preliminary " love play " in which the male strikes the female a number of blows with his abdomen, in a hammer-like manner and apparently with some force; meanwhile the genitalia of the male are extended visibly, the female offering no resistance and apparently accepting it as a normal proceeding.

When the female is ready to accept the male she raises her abdomen and union is almost immediately effected. For a while after copulation commences the antennae of the male are held close against the front of the head but later are extended, sometimes first one and later both ; the antennae of the female are extended all the time.

The time spent *in copula* is usually from ten to twenty minutes, but matings as short as two minutes and as long as seventy-seven minutes have been recorded, the average duration in 1,015 matings having been 15·98 minutes (Table I).

It was observed early in the rearing work that a male would mate on more than one occasion, both with the same female and with different females. When mating occurred more than once with the same female there was either a complete separation of the flies with a loss of position of the male, or only a short interval in what could be mistaken for a continuous mating, the male remaining in position on the female during this time. Mating with different females on different days occurs also, and the data obtained in such instances showed that each female was fertilized, but there was a definite indication that the number of larvae produced gradually lessened.

TABLE I.

Showing Duration of Matings of Metagonistylum minense.

Copulation in Minutes	1933				1934						Total
	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May.	June.	
— 5	1	—	5	—	—	—	—	—	—	—	6
—10	3	1	29	12	16	7	14	6	5	3	96
—15	5	16	46	32	39	48	57	53	53	63	412
—20	3	6	19	22	36	29	44	28	40	43	270
—25	—	3	3	9	13	9	14	36	26	16	129
—30	1	1	—	3	5	6	3	10	13	8	50
—35	1	1	1	5	2	3	5	1	4	2	25
—40	—	—	1	1	1	—	4	3	1	2	13
—45	—	—	—	—	—	—	2	—	—	1	3
—50	—	—	—	—	1	—	1	—	1	1	4
—55	—	—	—	—	—	—	—	—	—	—	—
—60	—	—	—	—	—	—	—	1	1	—	2
—65	—	—	—	—	2	—	—	—	—	—	2
—70	—	—	—	—	—	—	—	—	1	—	1
—75	—	—	—	—	—	—	—	—	1	—	1
+	—	—	—	—	—	—	—	1	—	—	1
No. Pairs ...	14	28	104	84	115	102	144	139	146	139	1,015
Total minutes	195	421	1,226	1,288	1,873	1,541	2,321	2,491	2,600	2,252	16,208
Copulation minutes—average ...	13·9	15·0	11·8	15·3	16·3	15·1	16·2	17·9	17·8	16·2	15·98

Females also have been observed to mate more than once, but in every such instance these matings occurred on the same day with short intervals only, and it would appear that such matings must be regarded as incomplete matings in the first instance rather than independent matings as in the males.

The all-important factor in mating is the intensity of the light. In previous work on TACHINIDAE some stress has been laid on the size and type of cage used for the flies in order that mating may take place readily. When work with this insect was commenced, bearing this in mind, comparatively large cages were used, but it was soon found that mating occurred frequently in much smaller cages, and it became evident that some other factor was involved. Investigation suggested intensity of light, and further work which followed confirmed this. Later, when the correct intensity of light was ascertained, it was found possible to obtain matings at almost any time of the day and in receptacles of any size, provided that the required intensity of light was obtainable, so much so that for laboratory purposes females were usually mated in 6 × 1 inch specimen tubes.

When mating is about to take place, as soon as the required intensity of light is attained the flies become active, this activity being a peculiar restless movement which is characteristic. Should the light either increase or decrease in intensity this activity at once ceases.

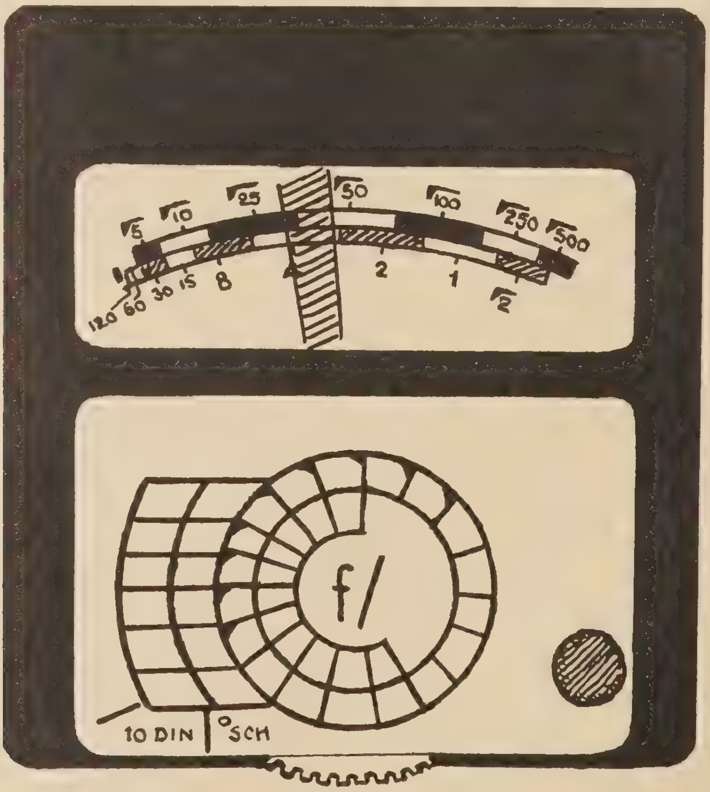

Fig. 1. Sketch of Sixtus photo-electric exposure meter showing intensity of light (shaded area) at which matings of *Metagonistylum* occur. The details of the meter with regard to emulsion speeds and f/values are not shown as they have no bearing on the intensity of light with regard to matings of the fly.

At first in order to standardise conditions the intensity of light was tested by means of a photographic exposure meter of the actinometer type, for want of a better instrument. The meter used was a simple comparator type, the Watkin's Bee Meter, which gave quite satisfactory results for general purposes.

It has been possible since to carry out tests of the intensity of light at which mating occurs with a Sixtus photo-electric meter. From a series of such tests it has been found that mating occurs in lights of an intensity within the comparatively narrow limits, on this meter, of the upper portion of the 25 area (needle in line with figure 4 on lower scale) and the lower portion of the 50 scale (needle at end of 4 area on lower scale) but usually about the upper end of the 25 area. In lights of intensities of either below or above the mating range the flies are usually quiet, thus at about the lowest quarter on the 25 area (25·1–25·2), as the lower extremity of the scale, and the highest quarter in the 50 area (50·6–50·7), as the upper extremity, mating activity ceases.

Gestation.—About six days after fertilisation the female fly is capable of depositing eggs. It is presumed that under natural conditions the fly would commence ovipositing as soon as this was possible and that each day such ova as were sufficiently developed would be deposited. For laboratory rearing it was found better to allow the female to go a couple of days longer before dissection in order to obtain a maximum of larvae for infestations.

Reproductive capacity.—The reproductive capacity of the Amazon Fly is considerable. Dissections undertaken to determine this showed that a total of as many as 991 ova and larvae may be contained in a single female, and as few as 180 ova and larvae. The mean capacity of 100 females was 559·1 ova and larvae, and 188·7 ova and 368·7 larvae, with an average mating time of 17·8 minutes. Table II gives the data in this connexion.

The duration of mating does not appear to have any effect on the number of ova and larvae produced by a female. The longest mating in the 100 females was of 50 minutes duration and the contents of the uterus on dissection in this instance was 310 larvae and 257 ova (total 567), while the individual with the shortest mating, of only 7 minutes duration, contained 505 larvae and 235 ova (total 740) ; in both instances the dissection was made on the seventh day after mating.

TABLE II.

Showing Reproductive Capacity of Amazon Fly.

Month	No. of flies	Minutes mating—average	Contents of uterus—average		
			Larvae	Ova	Total
1933 December ...	16	15·9	322·1	144·2	466·3
1934 January ...	31	19·6	421·3	145·1	566·4
February ...	26	15·7	449·3	184·4	633·7
March ...	11	14·7	417·8	191·5	609·3
April ...	15	16·1	266·9	227·2	494·1
May ...	1	25·0	345·0	240·0	585·0
Total ...	100	107·0	2,222·4	1,132·4	3,354·8
Mean ...	—	17·8	368·7	188·7	559·1

Number of parasites per host.—In the rearing of the parasite in the laboratory host larvae were infested with one or two larvae according to the stage of development and size, with a preference on the whole for single infestations, especially when host larvae were obtained from an area in which the fly was already established. That this method gave satisfactory results will be seen from the recovery figures of the laboratories given later.

As to the number of parasites that will develop within a host under natural conditions, examinations have shown that with *D. saccharalis* as the host from 60 to 65 per cent. of the larvae parasitized contain but a single parasite larva, from 25 to 30 per cent. contain two parasites, 6 to 7 per cent. contain three parasites, from 1·5 to 2·5 per cent. contain four parasites, and between 0·2 and 0·3 per cent. contain five parasites. In one isolated instance in the laboratory one host larva was found to contain 7 parasite larvae.

Habits of adult.—The adult fly emerges under laboratory conditions invariably in the morning hours between 8·30 and 11 o'clock, but emergence occasionally occurs in the afternoon also, about 1 p.m. and even as late as 5·30 p.m. The emergence of the fly appears to be dependent principally on temperature and humidity.

In the cages the adult fly will rest on cane leaves or grass placed therein for this purpose or on the mosquito-net covering, and in so doing often assumes a position head downwards, which may probably be considered their more general resting position.

In the field one does not often see the adult fly and then it is usually found resting on the underside of the cane leaves. The fly seeks this position for shelter from the sun during the heat of the day, and during rains also it has been observed to shelter thus. In the cooler periods during the morning and the evening they are to be found resting on the upper surfaces of the cane leaves and weed grasses in or near the fields.

In the cages in the laboratory the adult fly feeds readily on sugar, which was found preferable to syrup in which they usually became entangled and died as the result. White sugar (refined sugar or washed muscovado) proved preferable to yellow crystals; indeed, if fed on the latter, the mortality increased very considerably as well as the longevity being actually reduced. This high mortality with the use of yellow crystals was assumed to be due to the stannous chloride used in the process of making this grade of sugar, although it was never actually proved. Sugar of the dark crystal or muscovado grade (Java process) proved suitable for feeding also. Under field conditions feeding of the adult has not been observed.

As to the longevity of the fly nothing is known under natural conditions. In the laboratory flies have been kept for as long as 21 days, but the majority survived from 10 to 12 days. Some flies died as early as the fifth or sixth day after emergence, which in females would be before the period of gestation would be completed, assuming that mating took place on the day of emergence.

Host location.—In the location of the host there can be no doubt that the fly is guided by smell. Apart from the impossibility of seeing the host located, as it is within the cane, this has been amply proved in laboratory rearings.

At the beginning of the work when little was known of the biology of the fly and the number of flies on hand was very few, it was not advisable, nor in fact would the material available allow of it, to dissect flies for rearing purposes and flies were induced to oviposit in order to obtain an approximate time when dissections might be undertaken.

It was then found that flies with ovaries sufficiently developed would readily oviposit on a glass plate if a *Diatraea* larva was squashed and smeared on the plate;

in fact while they could be induced to deposit by this method they took little notice of a living *Diatraea* larva placed on the plate.

This method proved further that there was no selection on the part of the adult as regards host, for they deposited just as readily in the presence of smears of *Diatraea canella* larvae as in those of *D. saccharalis*. That the larva of the parasite will not develop with equal facility in these hosts is another aspect that will be dealt with later.

4. Species of Diatraea attacked.

Up to the present, *Metagonistylum* has not been recorded as attacking any genus other than *Diatraea* and, according to Myers (11), it attacks two species, namely, *D. saccharalis*, which he states is the " favourite host," and from which species the bulk of the material was obtained by him in the Amazon, and " another *Diatraea* apparently a new species allied to *D. impersonatella*, the most destructive small borer in Trinidad."

Although it was known that *Metagonistylum* attacked *D. saccharalis* at the time of its introduction into British Guiana, there was no information available as to whether the parasite would attack *D. canella*, the other species commonly occurring in this country.

The small amount of material in the early consignments did not allow any trials of this nature, and accordingly at the commencement of the work flies were released in fields regardless of which species of *Diatraea* predominated.

As soon as it became possible, however, this point was investigated and a series of infestations of larvae of both *D. saccharalis* and *D. canella* were carried out. The results of these infestations showed that, while a few larvae of *D. canella* may be infested artificially with the parasite, the large majority of fly larvae so used did not develop in this species. From a total of 6,523 *Diatraea* larvae artificially infested, comprising 3,503 *D. saccharalis* and 3,020 *D. canella*, the parasite recovery was 36·0 and 1·2 per cent. respectively. From that time *D. saccharalis* was used exclusively for laboratory rearings of the fly. It should be pointed out in this connexion that there is no actual difficulty in infesting *D. canella* larvae artificially, but the parasite larvae invariably fail to develop beyond the second stage, apparently owing to some physiological condition of that host.

The failure of some of the early releases of flies made in young ratoon fields in which there was a large preponderance of *D. canella* and in which recovery of the fly was not accomplished was also thus explained. Later, as the work became better organised, when an area was being stocked with the parasite, counts were made to ascertain the density of the *Diatraea* population and the preponderant species.

More recently as the result of inquiries of sugar planters as to whether the parasite would not eventually develop a strain that would attack *D. canella* more successfully, and if this desirable condition could not be arrived at by laboratory rearing, work was undertaken in this direction.

This work has already formed the subject of a paper by the writer (5), and it will be necessary to state here only that in rearings extending over a year and comprising three separate groups of material through ten generations with a total of 6,795 *D. canella* larvae artificially infested, an average of less than 4 per cent. produced puparia. There was no significant difference between either groups of larvae or generations and therefore no indication that the parasite could be reared in numbers on this host, nor of the development of a strain of the parasite more adapted to survival in this host species.

5. Colonisation of British Guiana.

Rearing the fly in the laboratory.—In the rearing of the fly in the laboratory the method followed was that suggested by Thompson (18) and successfully employed by Scaramuzza (15) and Box (2) in the rearing of *Lixophaga*, with such modifications as appeared necessary for this particular insect. For convenience a detailed account of the technique and the apparatus used will be given.

In the first instance gravid females which are known to have mated eight days previously are anaesthetised with carbon tetrachloride. As soon as the fly is dead, the uterus with its contained larvae is removed in physiological salt solution, the uterus being then ruptured and the larvae released in the salt solution. *Diatraea* larvae, previously collected from the fields, are then infested by placing upon them, by means of a small sable-hair brush, larvae of *Metagonistylum*. The infested *Diatraea* larvae are then placed in 1 oz. ointment tins (salve tins) where they remain for some three hours and are then transferred to young cane-shoots. The cane-shoots with the contained moth-borer larvae are then stored in special tin-boxes for a period of twelve days. Puparia obtained from these tins are kept for the emergence of flies, or balloon fly-traps are attached to the tins and the flies emerging are thus secured. From these flies a number of known mated females are retained for laboratory use, and the remainder liberated in the fields after a period of from five to eight days, being kept during this time in the mating cages, where further matings occur among the females not previously mated.

A modification which was adopted generally in the work here in British Guiana was to place *Diatraea* larvae directly into cane-shoots after they were infested with the parasite. This considerably shortened the work and the recovery of parasites from such larvae was equally as good as, if not in fact better than, with the tins.

At first large circular cages 24 inches high and 18 inches in diameter were used for mating, but later, when it was discovered that the size of cage did not affect mating, smaller cages were adopted and cages 18 inches high and 14 inches in diameter were used as standard. In these cages, under suitable conditions, mating takes place readily, and they serve also to store flies until they are liberated in the fields. These cages have four uprights and a single cross-bar at one end by which they are suspended, and were made of $\frac{1}{4}$-inch iron-rod welded at the joints. To each frame a bottom pan of galvanised iron with sides $1\frac{1}{2}$ inches high is fitted and wired into position ; the whole is enamelled white. A cylindrical cover of mosquito net, made to fit tightly and in the sides of which are two sleeves, is drawn over the frame and is closed by means of tapes at the top and bottom. When flies are being kept in a cage, a circular piece of gunny-bag (sugar bag) is placed in the bottom and this is kept constantly damp. Two glass receptacles (Syracuse watch-glasses), one containing sugar and the other a piece of cotton wool saturated with water, are placed in each cage, while in addition a bowl of water in which is standing grass (*Paspalum repens*) may be included.

It has been found that infesting the *Diatraea* larvae with the parasite is best accomplished by means of a fine sable-hair brush, and good quality water-colour brushes of No. 1 size proved very suitable. Further, in doing this, if a number of larvae are removed from the salt solution at one time and placed on a black plate in a vertical line, it facilitates the work of infesting, as they may readily be seen as they walk out of line about the black plate. By this method assistants are usually able to work without the aid of even a low-power lens, but for less keen eyes a circular reading glass about 3 inches in diameter mounted in a flexible arm proved a very useful aid.

Each *Diatraea* larva is wetted with a dab of salt solution before the parasite larvae are placed on it, and what was found to work even better was to keep the larvae (*D. saccharalis*) in glass tumblers and to transfer lots of 10 larvae at a time to a petri dish containing salt solution prior to infestation, the larvae being taken from this dish and infested immediately.

Should the *Diatraea* larvae be about full-grown, two parasite larvae are placed upon them (these are referred to as " doubles "), while if they are about third instar or rather undersized, they are infested with only one parasite larvae (" singles "). Small larvae are not infested.

If the tin method is used, a piece of blotting or filter paper wetted with salt solution placed in each tin greatly improves the chances of survival of parasite larvae which may drop or crawl from the host after it has been infested, and the infestation is greatly improved by this means. A thin coating of paraffin wax applied to the inside of each tin retards corrosion and so prolongs the useful period of these receptacles.

In the direct shoot method the infested larvae are placed in small cane-shoots in which a small pit has been cut previously, and as each larva is placed in the shoot and directly infested a small rubber band is placed round it to keep it closed. Subsequently shoots with infested larvae to a total of ten are slipped under one band, and they are placed in such bundles in the storage tins.

The cages used for storing cane-shoots containing infested larvae are galvanised iron cylinders (known as the " body ") to which are fitted tops and bottoms, and are of two sizes, namely 11 inches high by 10 inches diameter, and 11 inches high by 7 inches diameter. In each body about half-way between the top and bottom edges is cut a circular hole of 2¾ inches diameter around which is soldered a rim one inch high. The tops and bottoms are made to fit tightly inside the body so as to prevent the egress of *Diatraea* larvae, or when an outside cover is fitted a bead of about ¼ inch projection is inscribed around the body about 1½ inches from the top and bottom edges so that when the covers are in their places their edges come in contact with the bead, so making the body secure against the escape of the *Diatraea* larvae. To the circular opening in the body is fitted a cap of mosquito wire-mesh which affords ventilation to the cages and prevents excessive condensation of moisture within.

In storing the cane-shoots in these tins a layer of damp bagasse or sawdust is placed in the bottom pan and the shoots with the contained larvae stood upon this. It is essential to the production of parasite puparia that the moisture in these tins should be regulated to prevent the drying out of the shoots or the development of excessive moisture, which causes the formation of moulds. The temperature in these tins is surprisingly low and constant when thus prepared and is in the vicinity of 29–30°C. even when there is a good deal of heat being generated by the rotting cane-shoots ; the relative humidity being in the vicinity of 100 per cent. The storage tins are each numbered on the body, top and bottom, from 1 to 31 and the shoots stored therein according to the date of the month on which the contained larvae were infested, " doubles " and " singles " being kept separately for the purpose of working out the percentage of recovery.

After the cane-shoots have been stored thus for 12 days, balloon fly-traps are fitted to the opening, the circular cap being first removed, and in a day or so the flies commence to emerge. The balloon fly-traps fitted to these tins were of local construction and measured 9 inches long by 2¾ inches in diameter with a cone about 3 inches high, the top being made in the form of a cap which was readily removable to allow of the transference of the flies.

In practice, these balloon traps were often abandoned, however, and the puparia actually searched for by tearing apart the shoots. This was rendered somewhat easier than may be generally imagined by the decay of the shoots, and assistants with nimble fingers do not injure many puparia.

The puparia obtained are then placed on damp bagasse or sawdust in 2 lb. jam bottles covered with wire-gauze tops.

The method of storing in tins and securing the flies in traps, if it does not greatly increase the number of flies obtained, certainly effects a considerable saving in time, and on the whole is a marked improvement on the former practice, but for estate practice the searching method was generally preferred.

Mated female flies kept for laboratory use are confined in 2 lb. jam bottles from which the central area of the cover has been cut and mosquito wire-gauze substituted. In each bottle is placed a piece of blotting-paper on which there are a few crystals of sugar. One lb. jam bottles may also be used for this purpose and have proved entirely satisfactory. The sugar used must be either granulated white or dark crystal (muscovado).

It was found convenient when working in small spaces, as were most of the insectaries used in the work, to suspend the mating cages from the top of the insectary, and to arrange a counterpoising weight run over a couple of pulleys to allow the easy lowering and raising of the cages. The mating cages in the present instance weighed approximately 10 lb. and as counterpoising weights sash window weights or small bags filled with sand were used. Double-decked tables are also a great saving in space.

Temperature and humidity both play an important part in the artificial rearing of the insect (as will be observed from the statements made elsewhere in this paper) and must be regulated as far as possible. The methods used in obtaining the desired temperatures and humidities have already been mentioned. It remains only to say that in the storage tins for shoots the temperature was much less than would be generally imagined with the decay of shoots taking place therein, and was generally found to be about 30°C. while the humidity was in most instances nearly 100 per cent. R.H. In the laboratory temperature and humidity readings are taken three times a day, namely 8 a.m., 1 p.m., and 4 p.m., and there is also a self-recording thermo-hygrograph.

Laboratories.—A laboratory was erected for the investigation on the Sugar Experiment Station from a free grant made to the Colony by the Empire Marketing Board for the purposes of sugar-cane research. A portion of the equipment was also met from this grant. Later, with the actual introduction of the Amazon fly it was found necessary to enlarge the laboratory as well as to add to the equipment and apparatus, and this was met by funds provided by the British Guiana Sugar Producers' Association.

The laboratory as first erected was a small detached building 37 ft. long by 17 ft. wide, of wood framing and concrete stucco panels, raised on concrete pillars 3 ft. high ; a part of the building measuring 9 ft. by 17 ft. being screened with brass mosquito wire-mesh for use as an insectary. In order to protect the insectary against driving rains three small sloping glass roofs were affixed around the exterior. Later the building was enlarged by extending the insectary a further 10 ft.

On the sugar estates there has been a great diversity of type of insectaries, as might be expected, it being very often a matter of making an existing building serve the purpose ; thus we have worked in structures varying from what might be considered as ideal for a field laboratory with well-made benches and adequate apparatus, housed in a good building properly painted, to a structure that started its life as a large dog-kennel and immediately prior to the work was a calf-pen, with a low, leaky roof and roughly put-together benches of undressed wood.

The size of the insectaries used throughout the work both at headquarters and on the estates approximates 324 sq. ft., being roughly 18 ft. by 18 ft. With three assistants working, some 200 to 300 flies per day were produced in such laboratories, the number being regulated largely by supplies of *Diatraea* larvae from the fields.

Colonisation of the Sugar Estates.—At the time of the arrival of the first consignment of the parasite nothing was known of its bionomics, and the small number of flies (3) obtained from this shipment did not allow of any knowledge being obtained in this respect. So that when the second consignment arrived it was still unknown whether the insect would be amenable to laboratory rearing.

It was decided, therefore, to make liberations directly into fields of some of the adult flies emerging from the consignments pending the investigation of the bionomics of the insect and the matter of laboratory rearing. Accordingly, liberations of flies from the 3rd and 4th consignments were made in September and October.

At that time the weather was hot and dry, as is usual at this period, and *Diatraea* was generally scarce, and of those present *D. canella* predominated. No recoveries from these liberations were recorded and, as mentioned elsewhere, it is believed now that this was largely due to the preponderance of *D. canella* in the fields in which the liberations were made.

Liberations of this nature were made also with flies from the 5th and 6th consignments. During the first week in November (2nd and 9th) in a field of plant canes at Pln. Non Pareil (NP 29) 314 flies were liberated, and on 22nd November two puparia were found in a single bored shoot from which, on the following day, two Amazon flies emerged. Thus about three months after the arrival of the first flies in British Guiana the first recovery of the parasite was made.

In the meantime it was found that the technique which had been employed in connexion with the rearing of *Lixophaga* was also applicable to *Metagonistylum* and laboratory rearings had already been commenced. *Diatraea* had been infested in the laboratory as early as 21st September from flies of the 2nd consignment, which arrived on 12th September and from which the first flies emerged on the following day, and the first laboratory reared flies were obtained on 7th October, 1933.

From that date regular laboratory rearings continued. For the next eighteen months, and during the course of the work under the Colonial Development Fund grant, flies were reared and liberated on, or breeding stock supplied to, every sugar estate in the Colony.

Liberations having been made under suitable conditions, it was usually but a few weeks before recovery of the parasite could be made.

At the commencement the headquarters laboratory undertook the rearing of all flies and supplying of estates, the *Diatraea* larvae for use in the laboratory being sent in by different plantations. As time went on it became evident that if the entire sugar-growing area was to be stocked within a reasonably short period it would be necessary to produce much greater numbers of the fly than the facilities of the headquarters laboratory would allow. Accordingly, the co-operation of the sugar estate authorities was sought, and readily obtained, and arrangements were made to start rearing the insect in field laboratories on certain of the larger plantations. Assistants for work in these laboratories were obtained from the estates themselves with the aid of the managers and these were trained in the technique of rearing the insects at the headquarters laboratory. Ten such field laboratories were thus established on estates. These laboratories, with the exception of Pln. Albion, were directly under the supervision of the writer ; the laboratory at Pln. Albion was under Mr. H. W. B. Moore, entomologist of that estate. These laboratories were established at centres that were some distance away from headquarters and to which it would have been difficult to send continuous supplies, or where the area under the control of one group was large and it was more convenient to do this. For the nearer plantations as well as the smaller ones, headquarters laboratory supplied flies up to March 1935, when the grant terminated and the writer went on leave.

Careful supervision was maintained over the work of these laboratories. A weekly report on the working of each laboratory was received and frequent visits were paid to them as appeared necessary. As to the efficiency of the work at these field laboratories it may be stated that it was generally satisfactory and in some instances it reached a very high standard, the recovery of puparia having reached as high as 96 per cent. larvae infested, while the recovery of flies reached 95 per cent. puparia.

Up to the time of the termination of the grant (March 1935) that is, at the end of eighteen months, some 195,677 flies had been reared in all laboratories. Of this number, 25,226 or 12·8 per cent. were produced at the headquarters laboratory.

Since that time some 180,020 more flies have been produced on the sugar estates, making a grand total of 379,697 flies produced in all laboratories over the period of two years since its introduction.

The actual number of flies which were liberated was, however, considerably less that the figures given above. As regards headquarters laboratory, a total of 25,339 flies was reared during 1933-35 and 18,174 were distributed, that is, 71·7 per cent. In addition, some 2,000 flies were used in the laboratory.

6. Cost of Introducing the Parasite.

It is difficult to state any exact figure of the cost of introducing the Amazon fly into British Guiana owing to the conditions and arrangements under which the work was carried out. Nevertheless, a figure, which for general purposes may be taken as representative of the cost of the introduction of the parasite, has been arrived at and in order to complete this record it is felt that it should be included here.

As has been stated previously, the British Guiana Sugar Producers' Association provided funds to the extent of £2,000 for the actual cost of the introduction. This amount provided for the purchase of a special launch for work on the Amazon and its transportation through British Guiana thence, the transportation of the personnel and supplies of the expedition, the pay of such members of the expedition as were specially engaged for the purpose, the expenses of collecting the parasite in Brazil and its shipment to the Colony, and the pay of the junior laboratory staff at Georgetown.

Other charges which should be included properly in the cost of the introduction, but which were in fact not thus charged but were paid either from Imperial, Colonial, or other funds, would be the salaries of both Dr. Myers and the writer.

Making allowances for such charges and also for some other incidental expenses, but not including previous ecological work done on *Diatraea*, the total cost of introducing the fly into British Guiana, as distinct from the colonisation of the estates, that is, for the work covering the period April to December 1933, did not exceed £5,000 ($24,000).

From the material received in the Colony it has been shown that 1,400 flies were secured, and basing the cost on this number only, the cost per fly was $17·10. In actual fact, by the end of December 1933, some 3,384 flies had been obtained (including 1,400 in original shipments) and of these, some 2,690 flies had been distributed to the sugar estates, and if the costs are worked on this latter figure of 2,690 flies, the cost per fly was only $8·92 or £1 17*s.* 2*d.*

7. Parasitism of *Diatraea saccharalis* in Rice and other Host-plants.

The Amazon Fly has been observed to parasitize *Diatraea saccharalis* in this Colony in other host-plants as well as sugar-cane. Only a few months after its introduction the fly was recorded as parasitizing *D. saccharalis* in the rice fields adjacent to the Sugar Experiment Station where the headquarters laboratory was situated, and later it was recorded in this host-plant in other localities as well.

Since that time there have been observed a number of instances of parasitism of *D. saccharalis* in rice. During the past year this parasitism appears to have increased, but no data are available to confirm this.

That *D. saccharalis* in rice should be attacked is not surprising ; in fact, it was what was expected, for the aquatic nature of the crop offers conditions which it seems would be favourable to the development of the fly. The importance of this lies in the fact that rice, which is the second important crop of the Colony, is at times seriously attacked by *D. saccharalis* and at all times acts as an important alternative crop for the pest.

On sugar estates either in cane-fields or rice-fields or in their immediate vicinity, the Amazon fly has been recorded also as attacking *D. saccharalis* in the grass hosts *Echinochloa polystachya* (HBK), Hitch., *E. crusgalli cruspavoris* (HBK), Hitch., " Bamboo Grass," *Hymenachne amplexicaulis* (Rudge), Ness., " Bissy-bissy," *Cyperus articulatus*, L., and Para Grass, *Panicum barbinode*, Prin.

8. Status in 1937.

Examinations made on sugar estates at different times after the introduction of the Amazon fly into this country showed long since that the insect had established itself not only in sugar-cane but also in rice, and as regards the former crop at least was parasitizing a fair proportion of the *Diatraea saccharalis* in that host-plant.

A survey carried out about the middle of 1935 by Mr. F. A. Squire, while engaged as Supernumerary Entomologist in this Department, showed further that some two years after the introduction of the parasite and the colonisation of the sugar estates the insect was still doing good work. The results of this survey were not published.

About a year ago it was considered desirable to undertake another survey, and in January 1937, the work was commenced, continuing, as opportunity allowed, to January 1938. In the survey it was not possible to carry out examinations of all the sugar estates in the Colony, but fifteen sugar estates were examined extending from Pln. Skeldon on the extreme east of the Colony to Plns. Versailles and Schoon Ord on the West Bank of the Demerara River. It is believed that the number of estates examined and the area over which they are extended are sufficient to allow the results to be considered as being representative of the general conditions over the sugar-growing area.

As regards Pln. Albion, Berbice, the survey of that estate was carried out in conjunction with Mr. H. W. B. Moore, entomologist of that estate, who undertook the field collections of material.

A total of 212 fields was examined, comprising 88 plant fields, 54 first ratoons, 56 second ratoons and 14 third ratoons. In 155 fields (73·1 per cent.) the Amazon fly was found parasitizing either *D. saccharalis* or *D. canella* or both, 144 fields showing a parasitism of *D. saccharalis* only, but no field was found in which only *D. canella* was parasitized.

In these fields a total of 37,332 " deadhearts " were cut out, of which 20,998 or 56·3 per cent. were empty. Of the remainder, 14,274 (37·9 per cent. of the total) contained living *Diatraea*, in the proportion of 6,271 or 43·9 per cent. *D. saccharalis* (the black-headed borer) and 8,003 or 56·1 per cent. *D. canella* (the yellow-headed borer) ; 2,060 or 5·5 per cent. of the " deadhearts " were the result of other causes, including white grubs (hard-back beetles) and rats.

In 5,371 *D. saccharalis* found in positive fields, 863 (16·0 per cent.) were found to be parasitized by the Amazon fly at the time of examinations of the fields, the parasitism ranging from 3·4 per cent. to 36·2 per cent. While of the total of 212 fields, 39 (18·4 per cent.) showed parasitisms of *D. saccharalis* of 30 per cent. and over. If, however, all the fields examined are included, both positive and negative, the parasitism works out at 13·7 per cent. *D. saccharalis*.

The parasitism for *D. canella*, as expected, was low, 0·32 per cent. for positive fields and 0·23 per cent. for all fields.

Records were kept during the survey as to the number of parasites per host. Of a total of 863 *Diatraea saccharalis* records, it was found that 513 or 59·4 per cent. contained only a single parasite, 263 (30·5 per cent.) contained two parasites, 66

(7·6 per cent.) contained three parasites, 17 (1·9 per cent.) four parasites, and only 4 (0·5 per cent.) contained five parasites per host.

The puparia of the fly found in the field agreed very closely with these figures and were in the proportions of 59·4, 31·4, 7·5, 1·4 and 0·3 per cent. for one, two, three, four and five parasites per host respectively.

In January 1937, Mr. H. W. B. Moore recorded a hyperparasite of the Amazon Fly from Pln. Albion, Bervice.

This appearance of a hyperparasite was not unexpected, for it had long been known that the native fly parasite of *Diatraea*, *Leskiopalpus* (*Stomatodexia*) *diadema*, Wied., was attacked by the hyperparasite *Signiphora dipterophaga*, Girault, and the possibility of this insect attacking *Metagonistylum* was well recognised at the time of the introduction of the Amazon fly. This was confirmed when a determination of the insect was made by Dr. C. Ferrière of the Imperial Institute of Entomology.

In addition, Squire (16), in his report of 1935, had mentioned the finding of a puparium of *Metagonistylum* which had apparently been attacked by a hyperparasite, although he did not obtain any specimens of the insect.

Accordingly, during the survey, precautions were taken to secure hyperparasites in order to obtain data as to the prevalence of the insect.

On four estates of the fifteen the hyperparasite was obtained, namely, Plns. Port Mourant, Albion, Diamond and Farm. This would indicate that the hyperparasite is well distributed over the sugar area.

Of the 45 fields examined on these estates, in 13 (29 per cent.) hyperparasites were found, while of 178 puparia collected, 17 (9·6 per cent.) produced hyperparasites. If, however, the whole Amazon fly population of these fields is considered, namely 516 larvae and puparia, the percentage destroyed by hyperparasites would be only 3·3 per cent.

Commenting on the larval parasitism, Myers (11) in his review of the *Diatraea* situation in British Guiana in 1931, stated that the combined parasitism of the eight important parasites was 6·9 per cent. of the borers in cane. The larval parasitism by the Amazon fly of 16·0 per cent. *D. saccharalis* in the present survey must, therefore, be considered as very satisfactory.

9. Shipments of the Parasite to the West Indies.

While perhaps not strictly within the scope of this report, in order to make the account of the work in the Colony complete, opportunity is taken here to make mention of shipments of the Amazon fly which have been made from British Guiana since its establishment here.

St. Lucia.—As the result of a request from the Sugar Planters of St. Lucia, B.W.I., to the British Guiana Sugar Producers' Association, a shipment of puparia of the Amazon fly was made to that island in November, 1934. The shipment was made by the writer direct to Mr. Harold E. Box, entomologist engaged under the Colonial Development Fund, who was at the time stationed in St. Lucia (3).

Two hundred and twenty puparia of the fly were despatched by air mail from Georgetown on 27th November 1934, and arrived at St. Lucia the following day. Mr. Box subsequently reported that the puparia were received in good condition. Rearings of the fly were undertaken and the establishment of the insect in St. Lucia has formed the subject of a report by Mr. Box.

Puerto Rico.—In December 1935, Mr. S. M. Dohanian, of the Puerto Rico Experiment Station of the United States Department of Agriculture, came to the Colony to obtain material of the parasite for shipment to Puerto Rico. Mr. Dohanian remained in the Colony until February 1936, during which period some 6,000 adult

Amazon flies were sent by him by air mail to Puerto Rico. Consequent on the failure of the fly to establish itself in Puerto Rico, Dr. K. A. Bartlett, also of the Puerto Rico Experiment Station, visited the Colony in September 1937 and made further shipments of the fly to Puerto Rico.

Trinidad.—At the request of the Director of Agriculture, Trinidad, and with the approval of the British Guiana Sugar Producers' Association, shipments of the parasite totalling some 800 puparia were made to Trinidad in September and October 1936. These shipments were made by the writer and were received by Mr. A. H. Pickles, entomologist, Department of Agriculture, Trinidad.

More recently, a further small consignment of flies was sent to Trinidad by Dr. K. A. Bartlett while he was in the Colony.

10. Acknowledgments.

Any account of the work with the Amazon fly in this Colony would not be complete without acknowledgment of the assistance which I received in one way or another during the period.

Firstly, I would mention Dr. J. G. Myers, with whom I was associated both in this work and for some period before, during which the purely ecological investigations on *Diatraea* were undertaken.

To the sugar planters of the Colony also I would tender my thanks for their ready and active help which was largely responsible for the success which attended both the *Diatraea* ecological work and the subsequent colonization of the sugar estates with the Amazon fly, and especially to Messrs. J. C. Gibson, G. E. Anderson, G. M. Eccles, W. H. Richards, D. Mowatt and R. B. Hunter.

Finally, I have to thank my laboratory assistants at headquarters laboratory as well as those on the sugar estates who readily put in extra time in order to make the work a success.

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THE SEASONAL AND ANNUAL INCIDENCE OF THE SHEEP TICK, *IXODES RICINUS*, IN BRITAIN.

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Introduction.

It has long been recognized that the tick, *Ixodes ricinus*, has a two-phase curve of seasonal activity in Britain, in so far as its principal host, the sheep, is concerned. The first phase occurs in the spring and terminates in late May or early June ; the second, which is a much less serious infestation, occurs during the period September–October. Tick infestation of sheep is relatively low during the summer months and practically absent during the winter. This seasonal incidence has been described by Meek & Greig Smith (1896), Wheler (1899), Stockman (1916), and MacLeod (1932).

The writer advanced a theory (1936), based on laboratory and field evidence, that this periodicity is related primarily to temperature conditions, the ticks forsaking the tips of vegetation above and below a certain range of temperature, and so becoming less accessible to their hosts.

During the years 1930–1938 serial estimations of the degree of tick infestation on sheep were made each spring except in 1933, in one or more of the principal tick-infested areas of Scotland and England. Except where otherwise stated, the writer was personally responsible for the tick counts.

The method used throughout this investigation was to count the numbers of adult female ticks attached to the head, neck, chest and forelegs, including axillae. Except for a few attached to the bare parts of the abdomen and hind legs, the ticks on the areas mentioned represent practically the entire adult female population on a full-fleeced sheep, and by confining examination to these areas it was possible to examine large numbers of sheep at a time. This was an important consideration, since most of the estimations were made in connection with chemical control experiments, which usually involved from five to ten or more groups of experimental sheep. Ten sheep were usually counted for each estimation, and the figure given is the average for these counts. Since it is known that tick infestation may vary from one part of a farm to another, and between sheep of different ages on the same ground, the same group of sheep was utilized wherever possible throughout each series. In many cases, where the counts were made as incidental to tick-control experiments, the same ten individuals were counted each time.

The Meaning of Tick Activity.

Before proceeding to describe the results obtained, it is necessary to make clear what is meant by the term tick activity. In the earlier accounts of tick bionomics, this term is obviously intended to refer to the infestation of the host, and in this sense the writer has used it. It has not been used with reference to the physiological condition of the individual organism. Thus, the statement that " ticks are inactive " at a given season with regard to the sheep host means that they are not normally found on this host at that season, and not that they are in a condition of suspended animation. A German worker, Totze (1933), has suggested that a true diapause condition occurs, the species entering, during the winter months, a phase of continuous dormancy which is not affected by changes in weather conditions. The writer has given evidence (1932, 1935), to show that, in Britain at least, this diapause condition does not occur, and that physiological activity in this species is a simple function of temperature, irrespective of the season. There is no justification for the assumption of Hendrick and his collaborators (1938) that, following a snowstorm in December, ticks should be expected to be inactive for the remainder of the winter, for nowhere in the literature is there any record of such hibernation occurring in this country, and a body of evidence exists to show that it does not occur, but that observed inactivity in winter is due simply to the low temperature prevailing at the time of observation, and may be interrupted at any moment by weather conditions favourable for activity. Similarly, reduced activity in summer does not mean that ticks are dormant, as is sometimes supposed, but merely that the degree of infestation is markedly reduced.

Seasonal Activity of Ticks on Sheep.

Thirty-five series of tick counts were made, on twelve farms in Scotland and northern England. The farms chosen are fairly evenly distributed over the territory where ticks have long been recognized as a serious scourge, and should, therefore, yield evidence representative of the tick infestation conditions over the area in question. Of these thirty-five, nineteen were in four groups of adjacent sheep walks, and in these cases only one from each group is illustrated. Fourteen of the curves are illustrated (figs. 1, 2, 3, 4, 5 and 10).

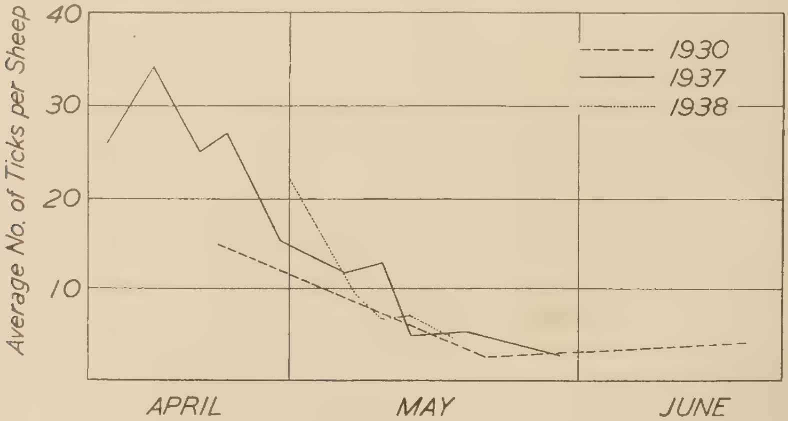


Fig. 1. Argyllshire : curves of tick incidence on sheep for three years on the same farm, showing the seasonal decrease in degree of infestation in early May.

In fig. 1 are given the curves of tick infestation, towards the end of the spring season of activity, for three years on the same farm in western Argyllshire. Unfortunately, no actual counts were made during the peak period in 1930, but the ticks at this time were assessed by the writer as " very numerous," and certainly exceeded fifteen per sheep on the 21st April. It will be observed that the tick numbers decreased rapidly during the first or second week in May in all three years.

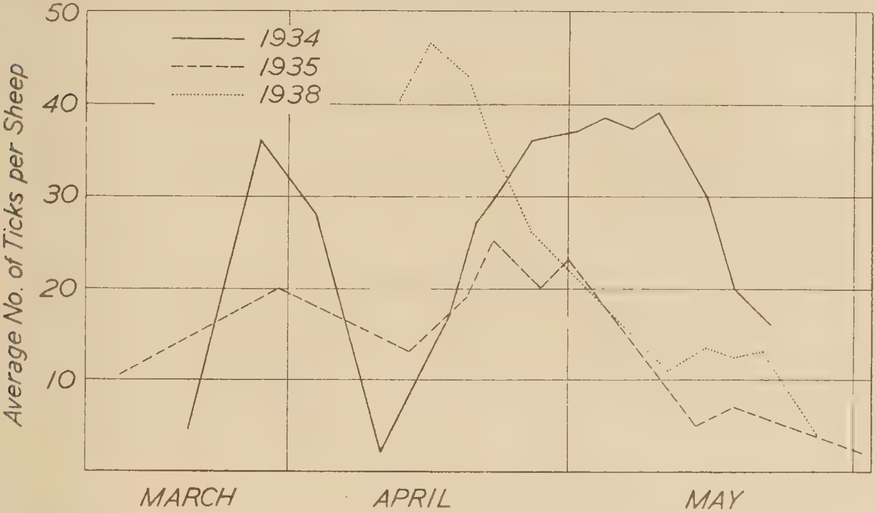


Fig. 2. Perthshire : curves for three farms, showing decrease in mid-May. In 1934 a reversion to wintry conditions, with snow lying for over a week, caused a sharp temporary drop in infestation.

Fig. 2 gives the curves for three separate farms, in different years, in central Scotland :—

1934, on the north-east side of Loch Vennachar.
1935, near Thornhill, Stirlingshire.
1938, in Balquhidder.

It will be seen that in these cases the tick incidence falls off about the middle of May, or during the first three weeks.

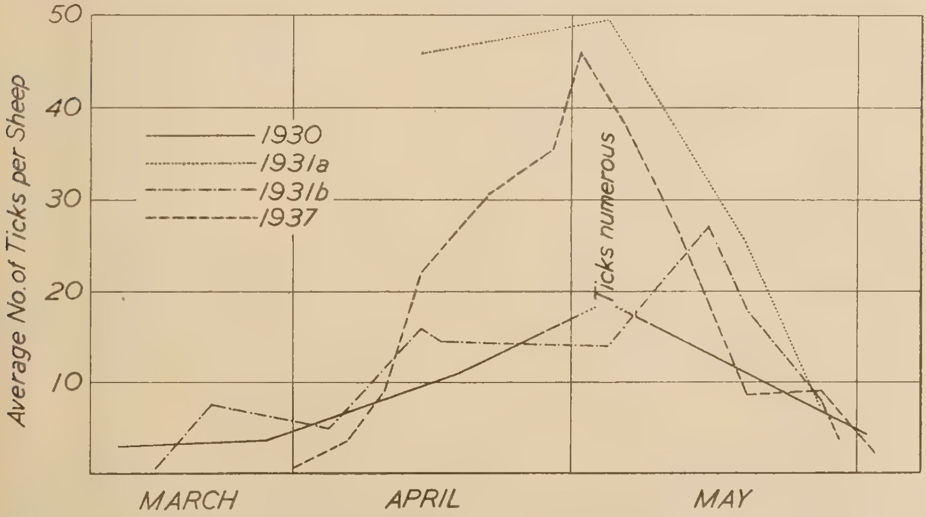


Fig. 3. Scottish Borders : four series of tick counts on a farm in the Ettrick Valley, showing decrease of tick infestation late in May.

In fig. 3 the curves for three years on one farm in the Ettrick Valley, Scottish Borders, are given. The 1930 curve is incomplete, ticks having been merely assessed as " numerous," during the second half of April and early May. The 1937 figures are taken from an article by Mr. Andrew Linton (Scottish Farmer, 19th February, 1938, p. 279). In this district the infestation appears to slacken later than in the west of Scotland, the curves decreasing to their summer levels during the second half of May.

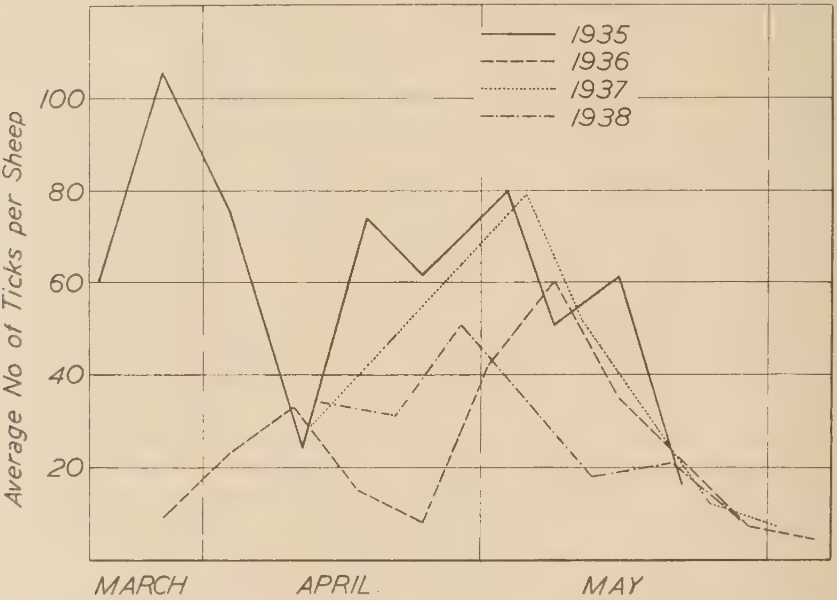


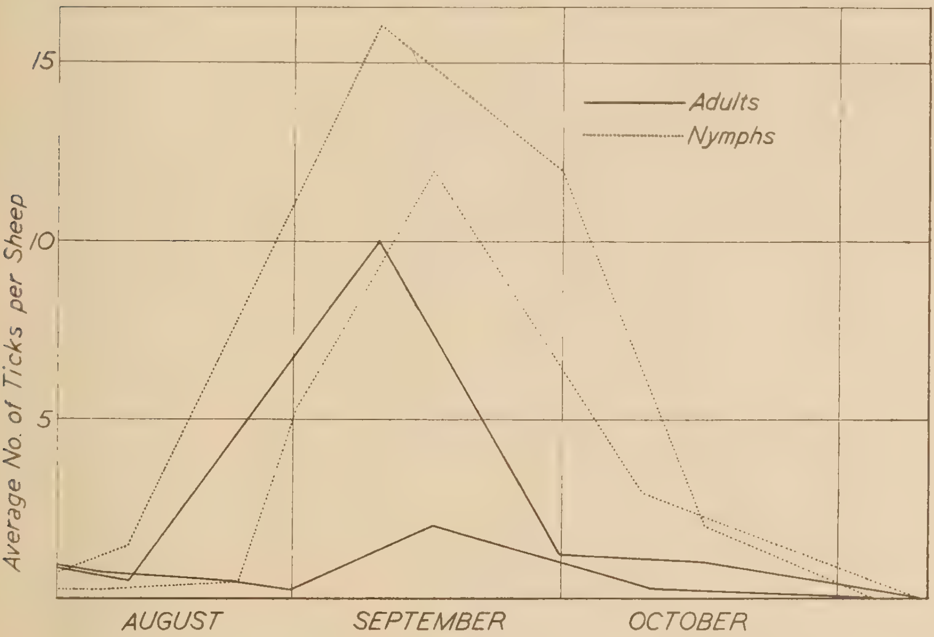
Fig. 4. Northumberland : four series of tick counts on farms in the College Valley and North Tyne valley, showing seasonal decrease in infestation late in May.

Fig. 4 gives curves for two areas in Northumberland. The 1935 and 1936 curves are for farms in the College Valley ; the figures for the latter were obtained by Mr. Lyle Stewart, of King's College, Newcastle, who also collaborated with the writer in obtaining the 1935 counts. The 1937 and 1938 counts were also obtained in collaboration with Mr. Stewart, on a farm in the North Tyne area. In the first three curves it will be observed that the infestation level dropped below 20 in the second half of May, as in the Ettrick district. In the 1938 curve there was a first decrease in early May, and a further decrease towards the end of the month.

From an examination of the foregoing curves, it is seen that on fourteen flocks under observation between 1930 and 1938 the tick numbers were found to drop rapidly during May from levels of between 15 and 100 to a point below 10, except in two cases where counts were discontinued early, and where the curves are clearly seen to be decreasing rapidly. In all the other cases, where serial counts were continued over a sufficient period, the results were in agreement with those illustrated. It is clear, therefore, that, over the principal tick-infested regions of Scotland and northern England, there is a well marked summer trough of low incidence of tick infestation which commences during May, or, rarely, early June.

An interesting confirmation of this periodicity is provided by an experiment on tick control carried out by the Cooper Technical Bureau in collaboration with Dr. Walton in North Wales. An account of this work has been published (Walton 1927). The figures for infestations by female ticks during 1925 and 1926 have been abstracted from the records. The 1925 figures are the counts made on the ewe stock, which was not being dipped that year. In the first count the two ewes with lamb have been omitted, as they had been on the hill for six days only. It will be seen that the incidence decreased in early June. The two points for 1926 are based on the female tick infestation of adult stock ; the first record was obtained before serial dipping commenced, the second nine days after the previous dipping, so that the protective effect of the dip should be negligible.

1925 : 8.v.25—10·5 ; 25.v.25—10 ; 10.vi.25—2·8
1926 : 7.v.26—11·2 ; 12.vii.26—1·6



The higher incidence of both adults and nymphs is for Argyll

Fig. 5. Showing autumn recrudescence of tick activity in Argyllshire and in the Borders.

Fig. 5 gives the autumn curves for females and nymphs on two farms, in Ettrick and western Argyllshire. These serve to illustrate the presence of an appreciable recrudescence of tick activity in autumn, which is, however, much less pronounced than the spring wave of activity. Further evidence of this autumn wave is contained in fig. 9 (Northumberland 1937), in that the ticks were reported to be so active in September that the whole flock was dipped in a special anti-tick bath.

The following records of examinations of sheep in the winters of 1930 and 1931 are given to illustrate the occasional finding of isolated ticks, or low infestations, although, in general, tick activity on sheep is absent during this season.

Ettrick.	9.x.30.	6	sheep	examined,	total of	1	female	and	3	nymphs.
	5.xi.30.	4	,,	,,	,,	0	,,	,,	0	,,
	16.ii.31.	5	,,	,,	,,	0	,,	,,	0	,,
	26.ii.31.	8	,,	,,	,,	0	,,	,,	3	,,
	6.iii.31.	3	,,	,,	,,	1	,,	,,	1	,,
	30.xi.31.	5	,,	,,	,,	8	,,	,,	0	,,
Argyll.	16.x.30.	6	,,	,,	,,	6	,,	,,	12	,,
	10.xi.30.	5	,,	,,	,,	0	,,	,,	0	,,

The Factors governing Seasonal Distribution of Tick Infestation.

Three theories have been advanced to account, wholly or in part, for the observed periodicity of ticks on sheep. These are :—

(1) The " two brood " theory.
(2) Totze's theory of a physiological rhythm in the metabolism of the tick.
(3) The temperature control theory.

Totze's theory, which was proffered as an explanation of the winter inactivity of ticks, has already been discussed. The facts that an appreciable, though low, infestation is often present throughout the summer, and that ticks are found on sheep in mild weather in winter, discount this theory as an explanation of the seasonal rhythm in tick activity.

Until the writer advanced his theory of a temperature control, the generally accepted belief was that the spring and autumn ticks represented two successive broods, those ticks which gorged in the spring completing their development during the summer and attacking sheep in their next stage in autumn. It was believed that the summer decrease was due to the spring crop of ticks becoming engorged, so that few or no ticks were left to infest sheep until these had moulted.

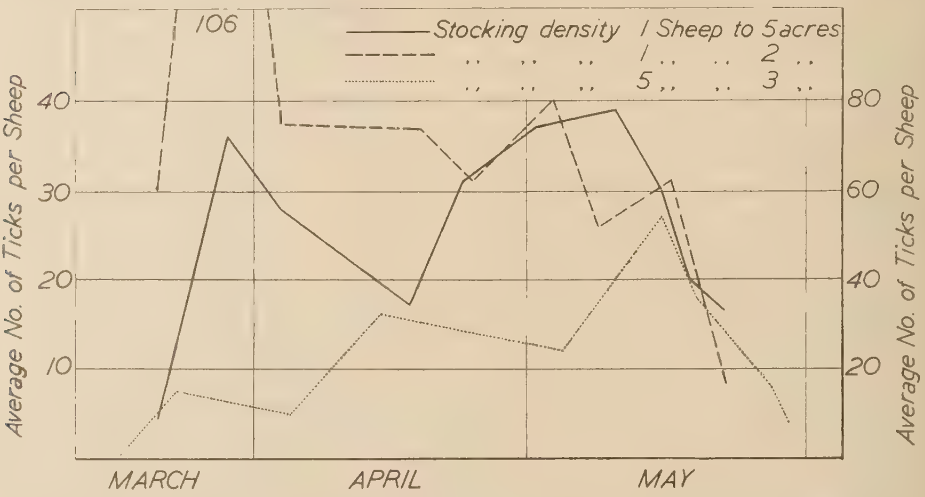


Fig. 6. The seasonal decrease in tick infestation in three flocks maintained at different densities per acre, showing that the time of decrease is independent of the stocking density. Because of the much higher incidence in one flock (density 1 to 2 acres), the curve has been plotted to a different vertical scale, which is shown on the right.

It is probable that some at least of the ticks infesting sheep in autumn result from ticks engorging in the spring, but the writer feels unable to accept the belief that the summer decrease is due to most of the available unfed ticks becoming engorged. Were this so, the termination of the spring period of high infestation would depend to a large extent on the density of stocking, heavily stocked ground becoming exhausted of its unfed tick population earlier than ground lightly stocked. Fig. 6, giving the incidence curves for three experimental flocks in which the stocking varied from five sheep to three acres to one sheep to five acres, shows clearly that the stocking density is not related to the time of relapse of the incidence curve.

In 1932 and 1936 the writer published figures showing the close correlation between tick activity and the weekly average of maximum air temperatures, as recorded at the nearest meteorological station. These figures, which are reproduced in fig. 7, suggest that the limits of air temperature (weekly maxima) for tick activity are 45°F. and 60°F. A reasonable criticism of this finding is that the air temperatures on the farms where the tick-counts were taken were not likely to correspond closely with those at the meteorological stations. In 1937 and 1938 further evidence was sought, and daily temperatures were read on two of the actual farms where serial tick-counts were being made, one in Argyllshire and the other in the North Tyne area.

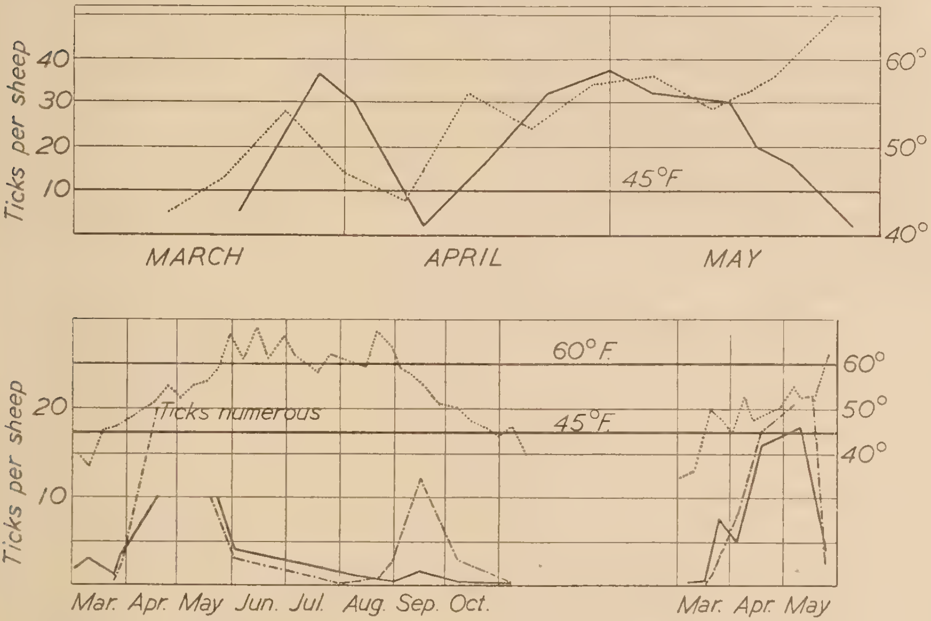


Fig. 7. The upper curves show the relation of tick incidence (solid line) to weekly maximum temperature (dotted line), on a Perthshire farm in 1934. The lower curve is for a continuous period of 15 months on a Selkirkshire farm. Both curves show the relationship of incidence to the air temperature limits of 45°F. and 60°F.

Fig. 8 shows the relationship between air temperature and activity in Argyllshire. In the 1937 curves it will be seen that the tick incidence, which had been ranging between thirty-four and twenty-five, decreased to eleven—fifteen when the average weekly maximum temperature approached 60°F. and, when the temperature exceeded 60°, dropped to levels of five ticks or less per sheep. The curves for 1938 are of special interest, and the daily temperatures have been given, to show more clearly the sequence of events. At the beginning of May the temperature dropped to unusually low levels, so that during the first week the maximum did not exceed 48°F. Tick activity decreased in this case on account of low temperatures. Between the 7th and 11th the temperature rose rapidly to 60°F. and subsequently remained above this level. It is suggested that tick infestation had not had time to increase to any marked extent during the period of rising temperature before it was again inhibited, this time by high temperature.

The curves for Northumberland are shown in figs. 9 and 10. The 1937 spring curves (fig. 9) show again a close relation between tick activity and average weekly maxima, the tick numbers, which had been over fifty per sheep, dropping to twelve and below, when the temperature passed the 60° limit. After tick-counts were discontinued, the farmer continued to record the air temperatures throughout the season. He reported that " odd ticks were observed at clipping (July 1st–4th)," and later wrote—" I thought perhaps you would be interested to know when the ticks came on to the sheep in the autumn, and I made a note of the date—September 10th. They were fairly numerous about the 23rd September, when we dipped all the sheep with

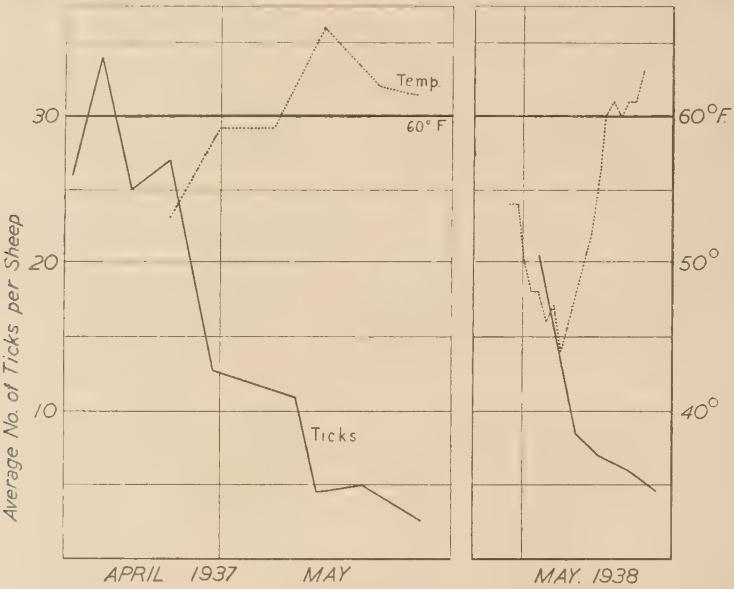


Fig. 8. Showing the relation between tick activity (solid lines) and weekly maximum temperature on a farm in Argyllshire, during the spring of 1937 and 1938.

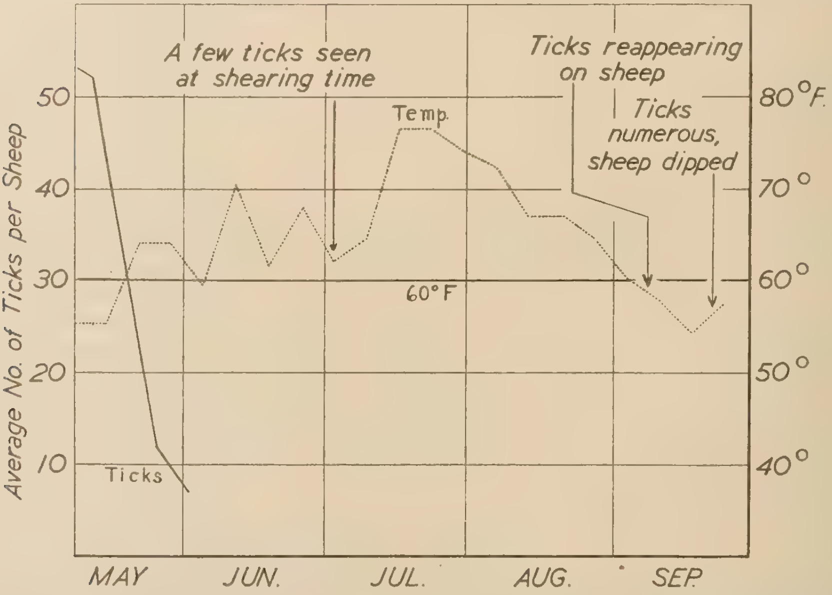


Fig. 9. The relation of tick activity on sheep to air temperature (weekly maximum), North Tyne Valley 1937. The upper limit of 60°F. is clearly shown both in spring and autumn.

Anti-tick dip." It will be observed that the weekly maximum curve crossed the 60°F. level during the week 8th–14th September. On the 23rd September the temperature was between 54·5° and 57·5°.

The 1938 incidence curve (fig. 10) shows several points of interest. The counts were made on a sheep-walk adjacent to that for which the incidence is illustrated in fig. 4 (1938).

For a week in the middle of March the temperature was above 50°F., and during this period the head shepherd reported that ticks were active on the sheep. Serial counts were commenced in the middle of April, shortly after the temperature had again risen from levels in the neighbourhood of the 45° limit, and the incidences continued to be high until the temperature reached 59°, when it dropped to low proportions. For the following three weeks the temperature hovered about the 60° limit, without crossing it except for one four-day period. The tick counts remained relatively low during this period, and were discontinued on the 28th May. Two counts were made by the head shepherd after the writer's return south, but unfortunately they were made on ewes, the infestation of which is known to be higher than that of hoggs exposed to similar conditions. Fortunately, however, two counts of ewe-infestation were made on the 10th and 28th May when the hogg-incidence was estimated, and these indicate the relative degree of infestation of ewes and hoggs. The ewe incidence curve for the end of the season illustrates the final decrease of tick infestation to summer proportions, after the average weekly temperature had definitely passed the 60°F. limit.

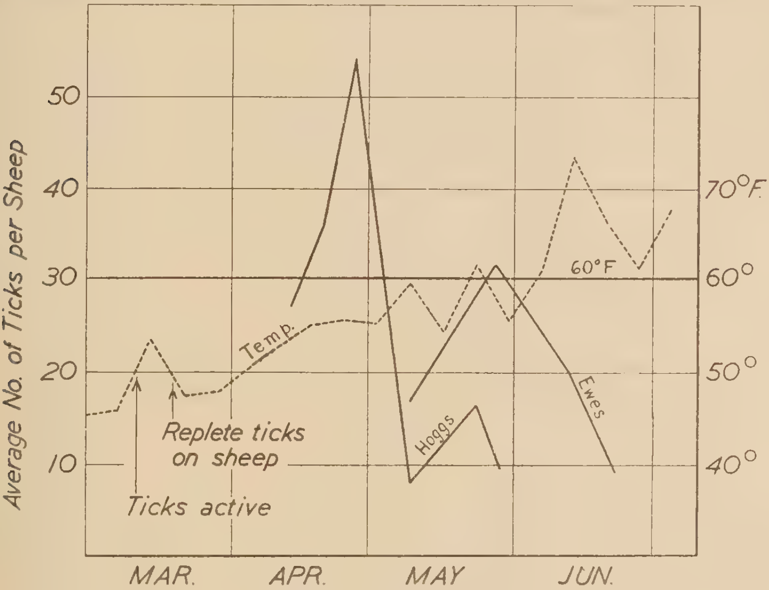


Fig. 10. North Tyne Valley 1938. Tick activity and air temperature (weekly maximum), showing the decrease in tick activity on sheep when maximum air temperatures approach 60°F.

Year to Year Variation in Tick Incidence.

It is sometimes stated that, over the country as a whole, the ticks are increasing in numbers, both by increase of density in areas where they have long been present, and by extension of the areas of infestation to hitherto clean ground. There are no experimental data available on the question of increase of infested territory, which will not, therefore, be further discussed here. A theoretical analysis of the conditions under which such increase may be expected to occur has been published elsewhere (MacLeod 1938).

Annual variation of the population level in a given area is at present difficult to assess accurately, for the index of population used, the incidence-level on sheep, is subject to a number of influencing factors, for none of which is the proper correction known. Thus :—

(*a*) The incidence of ticks on sheep may vary widely in successive counts. The number of ticks attaching each day has been shown to fluctuate with air temperature (MacLeod 1932), and tick infestation at any given time will, therefore, be more an index of weather conditions than of the true tick density on the pasture. Five successive weekly counts, on a farm in Northumberland, gave the following figures—60, 106, 75, 24, 74, *i.e.*, a range of 82 about an average of 68. It is clear, therefore, that no single count at present can be used as representative of an annual infestation level ; the full curve of incidence throughout the season must be given. Such a curve must have points no more than seven days apart, since female ticks may complete engorgement in seven days, and a sudden peak of high tick incidence, decreasing equally suddenly, might be completely missed by an observer making, say, fortnightly counts. In other words, every female which attaches to given sheep throughout the season should be counted to get a true picture of the annual infestation curve.

In illustration of the danger of comparing successive years on the basis of one count annually, the following actual figures extracted from the records may be given. They represent four successive counts each year for three different years.

	Count 1	Count 2	Count 3	Count 4	Average
Year 1 ...	15	14	27	18	18·5
,, 2 ...	20	13	19	25	19·25
,, 3 ...	36	28	2	17	20·75

The average for each year shows that the tick population was practically stable, yet an analysis based on the first count for each year would have indicated a steady increase, on the third count an equally definite decrease.

(*b*) For the plotting of an infestation curve as described above, care must be exercised that the sheep examined are always taken from the same part of the hill. The tick infestation of sheep on a given farm may vary widely between different fields or divisions of the hill. Since hill sheep remain on their recognised territories, it follows that samples taken at random from a farm flock may give completely misleading results. This variation between different parts of a farm is illustrated in the following figures, obtained on a Selkirkshire farm in 1935 :—

	Low Ground.		Hill.		
Date.	Fields.	Hillfoot.	Hill A.	Hill Valley.	Hill B.
23.iv.35 ...	—	—	—	24·2	—
30.iv.35 ...	100	43	47	18·4	—
7.v.35 ...	54·2	—	—	—	19·4
13.v.35 ...	35	—	—	—	—

(*c*) Care must be taken that the same class of sheep is used for each estimation. Marked differences exist in the degree of infestation of Blackface and Cheviot sheep on the same ground (Macleod 1932). Barren ewes and milk ewes show a difference in susceptibility, as shown by the following figures for average infestation, obtained from sheep grazing together on a Northumberland farm in May.

	Milk Ewes.	Barren Ewes.	Nos. of each class examined.
Area A	14	7	8
Area B	15·1	9·7	10
Average ...	14·6	8·5	—

The most marked differences occur between the infestations of hoggs (year-old sheep) and older ewes, exposed to the same conditions, and, further, the ratio of their infestations appears to vary during the tick season. Each of the following figures is the average of ten sheep :—

	Date.	Milk Ewes.	Hoggs.
Area B	13.iv.38	37·4	31·2
Area C	21.iv.38	24·7	13
Area C	10.v.38	17.2	7·9
Area C	24.v.38	27·1	16·5
Area C	28.v.38	31·7	9·6

To sum up, in our present state of knowledge, the infestation level in different years can be accurately compared only by making serial counts every seven days throughout each tick season, on the same class of sheep, running on the same part of the farm.

A very approximate idea of the relative population levels of different years may, however, be obtained by taking the highest average count obtained each season, on the assumption that the conditions under which that level was reached were the nearest approach to the optimum during that season. Judged by this criterion, neither the Perthshire nor the Northumberland infestations show a continuous trend, either of increase or decrease, between 1934 and 1938. In addition to the curves illustrated for Ettrick, two incomplete series of counts were made in 1932 and 1935. The highest figures obtained for the different years were 1931, 49·6 ; 1932, 45 ; 1935, 53 ; 1937, 46.

There is no indication here of an increase of density over an interval of seven years. The method, however, is open to so many objections that this result is of little value.

The Tick Incidence Curve for North-east Scotland.

In the course of an experiment at eradication of ticks from a grouse-moor in Aberdeenshire, a series of periodic counts was made, during the first year (1937), on certain undipped sheep of an experimental flock maintained on the moor. Daily readings of the maximum and minimum temperatures on the moor were recorded by the shepherds. Mr. W. Moore, of the Aberdeen College of Agriculture, who kindly supervised the experiment, personally undertook the tick-counts. To secure comparable results, the method of tick-counting adopted was uniform with that employed in the experiments already described.

The incidence curve obtained, and the corresponding weekly temperature maxima, are illustrated in fig. 11. This curve, which has been used (Hendrick *et al.* 1938) to prove the summer peak of activity claimed for north-east Scotland, is interesting in that it does not conform to the bi-modal type obtained on sheep farms elsewhere, and suggests the possibility that heavy tick infestation may, in fact, be continuous throughout the summer in this region. This explanation, however, involves the contingent assumptions that (1) the area was typical of sheep grazings in the north-east, and (2) that differences exist between the climates of this north-east area and other tick areas sufficient to account for the continuous high incidence, or, alternatively, that a marked physiological difference exists between ticks of the same species in two adjacent parts of the country. Before the explanation can be accepted, the validity of these assumptions must be established. It is of interest to review the existing evidence bearing on this rather curious discrepancy.

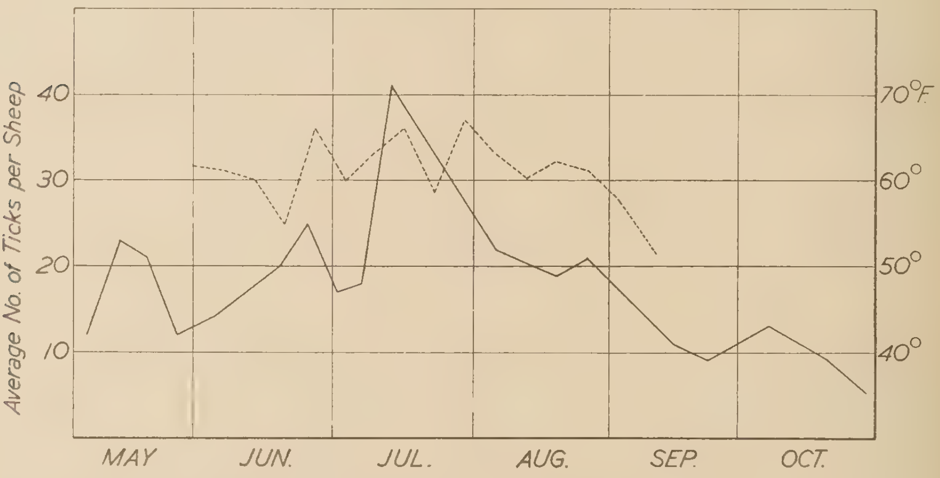


Fig. 11. Tick activity on sheep (solid line), and weekly maximum temperature on a grouse-moor in Aberdeenshire.

Assumption 1.—There are certain features of the experiment which leave the writer unconvinced that the tick curve should necessarily be a true reflection of the normal tick-incidence curve in the area. The moor in question is at an altitude of 1,000 to 1,500 feet ; there had been no sheep on it for ten years previously, *i.e.*, the tick population had been continuously bred for many years on hosts other than sheep —principally on hares and grouse ; the vegetation, not having been grazed down by sheep or cattle, was deeper and its elements coarser than that customarily found on hill sheep-pastures. It also consisted to some extent of unbroken patches of heather, which, in a normal grazing, sheep would avoid, but which the sheep had no alternative in this case but to enter. In these three respects the conditions were abnormal, and the possible effect of the differences on the tick-incidence should be investigated.

Assumption 2 (*a*).—In fig. 12 the monthly averages of maximum temperature for the months May to September are given for three stations in the north-east, viz., Braemar (1,111 feet), Logie Coldstone (608 feet), and Aberdeen (37 feet). For comparison, the maximum temperature curves for a station in each of the tick areas studied have been included. The stations are :—Argyllshire, Glenbranter (188 ft.) ;

Perthshire, Crieff (478 ft.); Scottish Borders, Eskdalemuir (794 ft.); and Northumberland, Bellingham (894 ft.).

It will be seen that the summer temperatures at Aberdeen are lower than those for the two inland stations, Logie Coldstone and Braemar, and these two are more likely to be representative of sheep grazings in the north-east area. The curves for both these stations are lower than those for stations in other areas, except Eskdalemuir, which is a bleak exposed moor. The difference, however, is slight, the summer temperatures at Logie Coldstone and Braemar being well over 60°F., and, therefore, if the ticks in this area behave similarly to those elsewhere, a summer decrease should normally be expected. The decrease would possibly be less pronounced than in other areas, and would theoretically be expected to commence rather later, *i.e.*, in June, since the temperature curves cross the 60°F. level later than those of other areas.

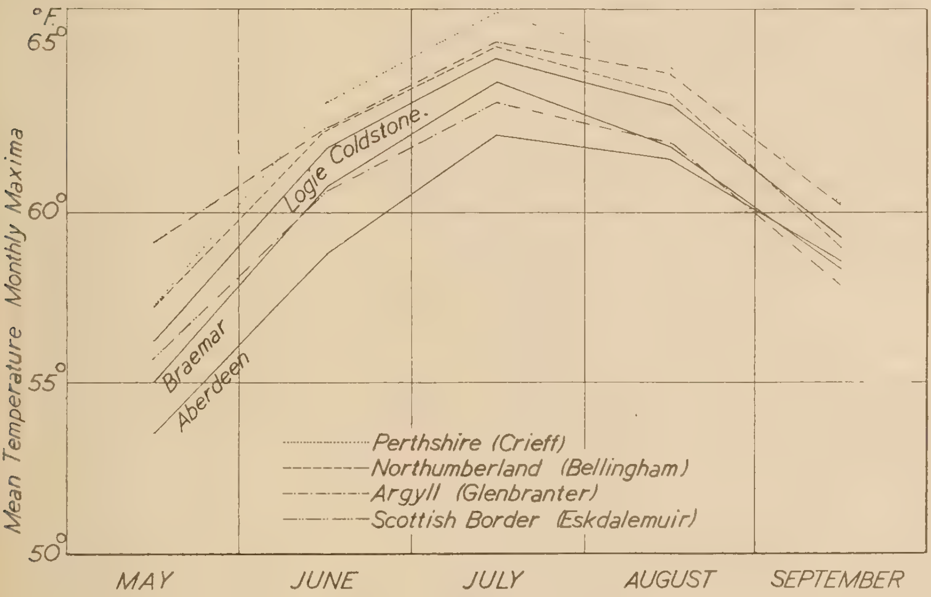


Fig. 12. The monthly averages of maximum temperature at three stations in Aberdeenshire (solid lines), compared with those of stations in other tick-infested areas.

Assumption 2 (*b*).—The curves in fig. 11 show that the tick incidence on the moor was greatest when the temperature curve rose above 60°F. This is completely at variance with the findings consistently obtained for sheep pastures, and, if the same result can be demonstrated for ticks on normal sheep grazings in the north-east, the evidence will justify the assumption that a physiologically different race of ticks exists in the area. The present evidence, however, is not sufficient for this, on account of the abnormal conditions under which it was obtained.

It may be of significance that the seasonal conditions on the moor were quite atypical; the weather until June was consistently cold and wet, with scarcely any growth of grass, and during the summer there were frequent clammy fog and cold winds on the hill. Another feature which may have a bearing on the explanation of the anomaly is that the herbage was longer than that on normal grazings. The temperature of the vegetation microclimate in summer is lower than that of the macroclimate. The greater depth of vegetation would allow to the ticks a greater vertical range of movement, and might possibly result in greater numbers being picked up on the bodies of sheep moving through the vegetation. This explanation, however, is scarcely adequate to cover the marked peak of tick incidence found in July.

Discussion.

It has been shown that, with the possible exception of the north-east of Scotland, tick activity on sheep in Britain appears to be represented by a two-phase incidence curve, the first peak occurring in spring and ending in May, the second occurring in September.

Examination at different times over a nine-year period has shown that the end of the spring phase is slightly later in Perthshire and distinctly later in the Border Hill country than it is in western Scotland. This cannot be due to a difference in breed susceptibility, since the only two breeds involved, Blackface and Cheviot sheep, occur in the three regions. Thus, in Argyllshire the principal breed is the Blackface; in Perthshire both breeds are met with; the Scottish Borders are principally Cheviot country; in the College Valley, Northumberland, both breeds occur, and in the North Tyne Valley the Blackface is again supreme. It is unlikely to be due to an earlier development in western Scotland of a physiological condition of the sheep's skin unfavourable to ticks, for seasonal physiological activities such as wool growth, judged by shearing dates, tend to be earlier, if anything, in the Borders than in the Scottish Highlands. On the other hand, there is a suggestion, in the limited evidence available, that the difference may be correlated with a climatic difference between the areas. Thus, in each of the two years 1937–38 in which temperature records were taken on the farms, the average weekly maxima first exceeded 60°F. during the second week of May in Argyllshire and the third week of May in Northumberland.

In fig. 7 the infestation seasons are seen to be defined by the maximum air-temperature limits 45° and 60°F. The correspondence between the upper limit of 60°F. and diminution of tick activity is further illustrated in figs. 8, 9 and 10. In figs. 8 (1938) and 10 the relation between activity and lower limiting temperatures in the neighbourhood of 45°F. is further demonstrated.

The known facts of seasonal incidence would thus seem to be most readily reconcilable with the theory of a temperature control of tick activity, the upper and lower limits being represented by average weekly air temperature maxima in the neighbourhood of 60°F. and 45°F. respectively.

Circumstantial evidence in favour of activity being limited to a given temperature range is found in the seasonal habits of ticks in different climatic regions. Thus, in north Africa, the southernmost limit of the distribution of *Ixodes ricinus*, the species is active only in winter, whereas in northern Russia, the northernmost limit of distribution, it is active only in summer (MacLeod 1936).

The theory of a temperature control of incidence was based on a laboratory finding that within a certain temperature range ticks were negatively geotropic, while above and below this range they reacted positively. It is suggested that, in nature, ticks climb the vegetation or descend to the roots according to the temperature. In spring large numbers of ticks are picked up from the vegetation on to the fleece, over which they wander until they find an attachment site. Summer temperatures are assumed to correspond with those found to produce a positive geotropism in the laboratory. Since ticks thus driven down into the body of the vegetation layer are still active, an appreciable number will still succeed in attaching to the nose or legs of browsing animals, or animals lying on them, and so an appreciable summer incidence is to be expected. This will be further accentuated by relapses of temperature in summer below the upper limit for activity.

Ticks which are at the root of vegetation in winter are at this season exposed to the inactivating influence of low temperatures, and will not normally be capable of attaching to browsing animals. It is known, however, that ticks inactivated by cold respond immediately to a rise in temperature by resuming activity, and so an occasional tick may be found on animals in winter, as a result of their activation either by the host lying on them or by a transient rise in air temperature.

In the case of sheep, a tick activated by the warmth of the animal's body would be unable, while the sheep continued to lie, to travel between the tightly pressed fleece and the ground, and once the sheep rose, it would have to travel over the surface of the fleece to one or other of the limited areas favourable for attachment. Since the temperature at the fleece surface, in longwool sheep in winter, is practically that of the surrounding air, and since the rate of movement of ticks is governed directly by temperature (MacLeod 1935), the tick would usually in such cases be inactivated before succeeding in travelling far. This would not apply to a hair- or fur-coated animal, to any part of whose body the tick can attach, and thus deer or fur-bearing animals might well be expected to have ticks attached more frequently and in greater numbers in winter than would sheep. In the case of deer a relatively high infestation is to be expected, on account of the habits of the species (MacLeod 1938).

Hendrick and his collaborators claim to have shown with regard to *Ixodes ricinus* in north-east Scotland, that " its activity differs very widely from that reported in other parts of the country," the difference apparently being that " tick activity is continuous throughout the year, the seasonal incidence being greatest in summer and lowest in winter." They state that, according to Wheler, Lyle Stewart, and MacLeod, " ticks are scarce during the summer months and completely inactive in winter."

With regard to the summer incidence, the evidence is interesting, but not yet conclusive, and it is much to be desired that serial estimations be made on the sheep flocks of normal sheep farms in the area. The second claim, of a unique condition of continuous winter activity, is untenable and would appear to have arisen from a misconception of the nature of the so-called winter inactivity of ticks. Further, Lyle Stewart (1936) and MacLeod (1932, 1936), both of them cited as stating that ticks are completely inactive in winter, explicitly state in the papers cited that ticks may be found on sheep in winter if the weather be mild, and the latter also gives (1936) as evidence of some degree of winter activity, the occasional occurrence of cases of louping ill. Stockman (1916), states " the fact is there is no time of the year in which at least some ticks may not be found on sheep running on tick-infested pastures." Brumpt (1922) also mentions the possibility of ticks occurring in winter in mild weather in France.

In support of their contention, Hendrick, Moore and Morison give the following figures :—

25th November,	average	infestation	of sheep	0·5	females.
27th January,	,,	,,	,,	1·5	,,
9th February,	,,	,,	,,	1·2	,,

It can scarcely be maintained that this evidence indicates a habit markedly different from that recognized by the workers cited above. The authors also record an infestation of 8·4 females per deer on 27th January. When it is remembered that deer, on account of their habits, are peculiarly liable to heavy infestation by ticks, so that a single animal may have, in the tick season, an infestation of 500 or 1,000 females, the figure would seem to support the accepted theory of a winter cessation of tick-activity.

The position may be summed up as follows. Occasional moderately warm days are met with in winter, and occasionally ticks are found in low numbers on sheep.

Both are atypical findings, and it is no more reasonable to claim from the latter that active tick infestation of sheep is continuous throughout the winter than to infer from the former that the winter is continuously mild.

Summary.

1. Serial examinations of the degree of infestation of thirty-five flocks during a nine-year period in Argyllshire, Perthshire, Selkirk and Northumberland, showed that tick incidence is greatest in spring and decreases markedly in early summer. Evidence is given of a similar periodicity in North Wales.

2. Evidence is given of the occurrence of a slight recrudescence of activity in autumn, and of the almost complete absence of activity in winter.

3. The spring curve of activity terminated in early May in Argyllshire, in the middle of May in Perthshire, and towards the end of May in the Borders and Northumberland.

4. The estimation of the relative annual infestation, *e.g.*, in relation to the question of spread or increase of ticks, by single annual counts is shown to be quite unreliable.

5. No evidence was obtained of an increase in density of ticks in any area during the period of observation.

6. The seasonal periodicity in activity was found to bear no relation to the density of stocking of the ground by sheep.

7. The seasonal activity of ticks in Argyllshire, Perthshire, Selkirkshire and Northumberland, was found to be related to the air temperature, expressed as the weekly average of maximum temperatures. The limits of the air-temperature range corresponding to active tick infestation are 45°F. and 60°F. (average weekly maximum).

8. The curve of tick infestation during 1937 on a moor in North-east Scotland was found to differ markedly from the normal, and the possible explanations of the discrepancy are discussed.

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NEW SPECIES OF BRACONIDAE (HYMENOPTERA).

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Imperial Institute of Entomology.

This paper deals with seven Indian species and one African variety belonging to the subfamilies Spathiinae and Doryctinae. Four of the species are important parasites of the cotton stem weevil, *Pempheres affinis*, Fst., and are described as new in compliance with an urgent request for their names.

Subfamily Spathiinae.

Spathius critolaus, sp. n.

♂♀. Head, thorax and petiole reddish-brown to yellowish-brown in the ♀; yellowish-brown in the ♂; basal third of tergite (2+3) more or less same colour as the lighter parts of the body; this pale area is more extensive and more sharply marked in the ♂ than in the ♀. Palpi pale yellow. Antennae markedly yellowish, the last 5 or 6 segments slightly paler; extreme apex of the flagellar segments darkened so that the flagellum appears finely ringed with black. Legs brownish testaceous, with the femora (especially the hind ones) slightly darkened on anterior and posterior sides; the legs of the ♂ are paler, but the hind femora usually show a dark patch on each side; coxae of both sexes unicolorous whether dark or pale.

♀. Macropterous. *Head* transverse, at most very slightly narrower behind the eyes than across them. Face faintly shining, evenly convex, covered all over with fine, smooth, parallel, transverse, absolutely even aciculation. Vertex almost smooth, at most with traces of transverse aciculation. Temples and cheeks completely smooth. Ocelli arranged in a triangle, the base of which is clearly longer than its sides. Ocell-ocular line slightly more than twice the distance between the posterior ocelli, 7 : 3. Antennae broken in type series, 25-segmented in the single ♀ in the series from the Punjab; flagellum 1 slightly longer than scape plus pedicel, 10 : 9 and slightly longer than f.2, 10 : 9. Clypeus not delimited. *Thorax*: mesonotum with a few, long, upstanding hairs; its lobes feebly shining, covered with a vague, scaly-reticulate sculpture. Notauli rugose. Scutellum rather sharply margined on each side. Pronotal keel very feeble, coalesced above with the posterior margin of the pronotum. Propodeum short, its posterior face fully as long as its dorsal face, though there is no sharp division between the two, without a distinct basal carina and areola, hence without delimited dorsal areas; the surface everywhere irregularly rugose. Mesopleurae with some sort of sculpture virtually everywhere; its furrow showing as a broad, shallow impression, crossed by striations which extend beyond its limits (the single ♀ from the Punjab has the mesopleurae much less extensively sculptured but nowhere is the surface completely smooth). Wings (fig. 2, **b**): radius arising very distinctly from beyond the middle of the stigma; 2nd abscissa of the radius as long as, or slightly longer than, the 1st transverse cubitus. Legs: front tarsus only a little longer than its tibia, 25 : 21; middle tarsus shorter than its tibia; hind coxa with a distinct projection beneath at base; outer apical margin of the hind tibia with a row of fine spines (fig. 1, **a**); hind tarsus 1 exactly as long as 2; 3 a little shorter than 5. *Abdomen*: petiole short, gradually widened from spiracles to apex, twice as long as its apical width, rugose, but becoming striate on apical third. Tergite (2+3) with fine striation almost to apex; this striation is predominantly longitudinal, except perhaps towards its apical limits where laterally it tends to be curved. Following tergites virtually smooth and shining throughout. Ovipositor sheaths half to two-thirds as long as the abdomen.

Length : 2·8–3·1 mm. (without ovipositor).

♀. Micropterous (fig. 1, **d**). In the type series the great majority of the females are of this form. The mesonotum is small by comparison with a fully winged female. Fore wing reduced to an elongate, scale-like stump which reaches to about the basal margin of the propodeum.

♂. Micropterous. All the males are of this form in the type series. Antennae 24-segmented (1 ♂, broken in others). The reduced wing is of the same form as in the female.

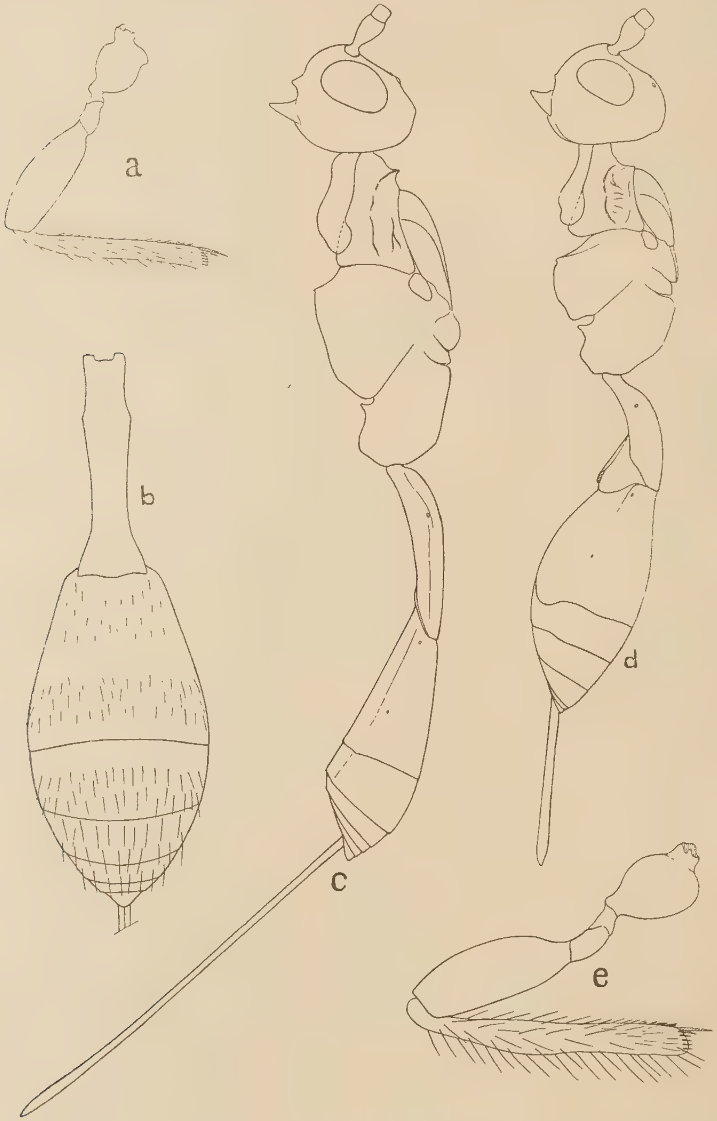

Fig. 1. **a,** *Spathius critolaus*, sp. n., ♀, part of hind leg ; **b,** *S. labdacus*, sp. n., ♀, abdomen ; **c,** *S. labdacus*, sp. n., ♀, body (lateral) ; **d,** *S. critolaus*, sp. n., ♀, body (lateral) ; **e,** *S. labdacus*, sp. n., ♀, part of hind leg.

♂. Macropterous. Males belonging to the series from the Punjab. Tergite (2+3), in addition to being pale at base, shows a yellowish spot on each side more apically; longitudinal sculpture of this segment tends to be broken up, in places, into a scaly-reticulate sculpture; as in the type-series, the sculpture of whatever kind extends almost to apex. Basal carina and areola of propodeum fairly well developed; but the single micropterous female in the series is like the females from S. India. Hairs of the outer side of the hind tibia longer and more numerous than in the micropterous males of the type series.

Length: ♂, 2·5–2·9 mm.

S. INDIA: Coimbatore, 7 macropterous ♀♀ (one the type), 56 micropterous ♀♀, 20 micropterous ♂♂, bred from *Sinoxylon* and *Pempheres* (*P. N. Krishna Ayyar*). PUNJAB: Chichawatni, 16 macropterous ♂♂, 1 micropterous ♀, bred from seeds of *Prosopis spicigera* (*S. D. Bhatt*).

This species is very closely related to *Spathius vulnificus*, Wilkinson (1931), which, as far as I know, is always fully winged in both sexes. The sculpture of tergite (2+3) is the most reliable character for separating the two species: in *vulnificus*, this segment has a pale, semicircular, basal area which has extremely fine aciculation but is sometimes almost smooth; the direction of the aciculation varies from longitudinal through convergent to concentric; in *vulnificus*, too, the 2nd abscissa of the radius is distinctly a little shorter than the 1st transverse cubitus. No confusion arises, of course, where micropterous forms of *critolaus* are concerned.

Both *S. vulnificus*, Wilk., and *S. critolaus*, sp. n., belong to a species-group which is essentially characterised by the very distinctive sculpture of the face.

Spathius labdacus, sp. n. (fig. 1, c).

♂♀. Reddish-brown with the abdomen blackish; there seems to be variation in the colour of the thorax, small individuals tending to have this part darker than larger ones. Maxillary palpi blackish with the apical segment whitish. Antennae yellowish, darkened towards the apex. Legs: all the coxae and femora reddish-brown like the thorax; trochanters and tibiae much the same colour as the femora but both sometimes blackish in small individuals; in other individuals the tibiae are blackened basally; middle and front tarsi yellowish with the apical segment darkened; hind tarsi usually darkened with only the base of the basal segment yellowish. Fore wings much darkened, marked with hyaline spots and bands as shown in fig. 3, b.

♀. *Head* decidedly a little flattened dorso-ventrally, though there is some variation. Face reticulate-rugose, clothed with silvery hairs. Clypeus triangular, with base longer than sides. Frons and vertex covered all over with fine, transverse, broken striation, the rugulosity of the sculpture being characteristic. Temples and cheeks with rugose-striate sculpture; in smallest individuals, the cheeks tend to become smooth towards the occipital margin. Vertex not rounded behind, the ocelli and uppermost point of the occipital margin lying almost in the same plane. Antennae with 35–39 segments; scape plus pedicel slightly longer than flagellum 1, 10 : 9; flagellum 1 to f.2 as 3 : 2. Eyes rather deeply emarginate on their inner side; ocell-ocular line to distance between posterior ocelli as 7 : 3. *Thorax*: pronotal keel free, well developed and, seen from the side, raised above the level of the posterior margin of the pronotum. Mesonotum not at all gibbose in front, sloping very gradually to pronotum, with sparse, upstanding hairs. Notauli somewhat superficial but fairly evenly crenate at least on anterior half; two nearly parallel, sometimes broken, ridges bound their inner margin on posterior half of mesonotum. Lobes of mesonotum in far greater part covered with close scaly-reticulation, feebly shining. Scutellum evenly convex, scaly-reticulate. Propodeum: basal carina usually about as long as its forks, but sometimes all ill-defined and broken; dorsal areas with fine surface sculpture posteriorly but merely rugose towards apex. Mesopleurae, immediately adjacent to the crenate-rugose furrow, sometimes nearly smooth but more often scaly-reticulate; upper half with more or less longitudinal rugosity; sub-alar impression of the mesopleurae weakly pubescent. *Wings*: submedian cell distinctly constricted before apex (fig. 3, **b**). *Legs*: front tibia to its tarsus as 5 : 7; middle tarsus 3/4 as long as its tibia; hind coxa rounded beneath at base; hind femur stout, abruptly narrowed on upper side at base (fig. 1, **e**); outer, apical margin of the hind tibia with a row of 4–5 small spines; segment 2 of the hind tarsus slightly more than twice 2, 17 : 8; 3 shorter than 5, 5 : 6. *Abdomen* (fig. 1, **b**). Petiole finely rugose, with indication of feeble, longitudinal wrinkles. Tergite (2+3) dull, finely rugulose all over, having almost a shagreened appearance; on about basal half, the sculpture is very slightly coarser. Following tergites dull, similarly sculptured to (2+3). Tergite (2+3) fairly sharply margined as far as the 2nd spiracle. Ovipositor sheaths about $1\frac{1}{3}$ times as long as the abdomen.

♂. Antennae with 36–42 segments. In small examples, the basal carina of the propodeum and its forks tend to be broken up and lost in the surrounding rugosities.

Length: ♂♀, 3·5–4·1 mm. (without ovipositor of ♀); type ♀, 3·6 mm. (without ovipositor).

SOUTH INDIA: Coimbatore, 2 ♂♂, 3 ♀♀ (one ♀, the type), ix.1937–i.1938; 6 ♂♂, 15 ♀♀; both series bred from *Pempheres affinis*, Fst., in *Triumfetta rhomboidea* (*P. N. Krishna Ayyar*).

This insect belongs to a group of *Spathius* of which I know of no other described species, though I am acquainted with two other forms from Borneo and the Philippines; these will be described in a revision of the Old World species of *Spathius* now in course of preparation. The group is characterised by the flattened vertex (admittedly not a conspicuous feature of the present species), by having the front and middle coxae the same colour as the hind pair, by the absence of a projection at base of hind coxa, by the pattern and venation of the fore wing, and by the dull, evenly sculptured abdomen.

Apparently, the facies of *S. labdacus*, sp. n., in combination with the sculpture of the vertex and the length of the ovipositor, provides the essential specific characters.

Subfamily DORYCTINAE.

Key to the Indian Species of Rhaconotus (♀♀).

1. Tergite (2+3) with a transverse, medial polished band, which separates the sculpture of the basal part of the segment from that of the apical part (fig. 2, **e**)........*signipennis* (Walk.)

Tergite (2+3) without such a band, its sculpture being continuous from base to apex or nearly to apex........2

2. Tergite (2+3) divided by two transverse furrows into three areas, the middle one transverse, fusiform, showing a sculpture different from that of the other two, being predominantly rugose-reticulate. Sp. with the mesonotum clothed all over, evenly, with very short, fine, inconspicuous hairs......*menippus*, sp. n.

Tergite (2+3) divided by one transverse furrow into two areas. Spp. with the mesonotum not thus clothed, whatever hairs present being concentrated along the course of the notauli and then, thick and conspicuous........3

3. Fore wing uniform in colour, almost hyaline with a yellow tint; stigma very pale yellow or yellow testaceous; propodeum with a sharp, well defined, basal carina and with some fine scaly-reticulation at least posteriorly on each side of this. Spp. having the vertex, pronotum and part of the mesonotum with a conspicuous clothing of thick, curved, glistening, whitish hairs; 2nd abscissa of the medius of the hind wing about $2\frac{1}{2}$ times as long as the 1st; hairs of the outer side of the hind tibia almost equal to the width of the tibia; propodeum apically, irregularly rugose-reticulate........4

Fore wing darkened in part and marked at least with a transverse hyaline fascia at middle ; stigma blackish, pale on basal third ; propodeum not as above. Sp. having the propodeum with a few obsolete, longitudinal, broken carinae, its entire surface, including that of the carinae themselves, overlaid with a glistening, more or less scaly-reticulate sculpture..............*cleanthes*, sp. n.

4. Antennae with 44–47 segments ; mesonotum a little longer than its greatest width ; dorsal areas of the propodeum not defined, their presence indicated basally by some fine sculpture between the basal carina and the inner, lateral carina. Sp. with the thorax markedly elongate, more so than in the next species ; hairs of vertex, pronotum and mesonotum a conspicuous and very characteristic feature ; Punjab, Mysore, Bihar, Bengal (parasite of *Scirpophaga*)..*scirpophagae*, Wilk. 1927

Antennae with 30–32 segments ; mesonotum a little shorter than its greatest width ; dorsal areas of the propodeum well defined, except apically, their presence indicated by a large surface of scaly-reticulation. Sp. with the hairs of vertex, pronotum and mesonotum much less characteristic ; Punjab (host : borers hibernating in wheat-stubble)..............................*oryzae*, Wilk. 1929

Rhaconotus menippus, sp. n.

♀. Dark brown, appearing blackish. Face reddish-brown. Eyes margined with reddish-brown. Palpi pale yellow. Mesonotum suffused posteriorly with reddish but this is not conspicuous. Legs honey-yellow throughout with sometimes a conspicuous reddish-brown tinge ; the colour of the legs seems to be variable. Fore wings very slightly and uniformly darkened ; stigma uniformly pale brownish-yellow, contrasting with the darker veins.

Head markedly transverse, very distinctly narrower behind the eyes than across them (fig. 2, **a**). Face shining, very finely rugose, with a transverse tendency in the sculpture, covered with fine, pale hairs. Cheeks and temples virtually unsculptured, smooth, at most a trace of surface-sculpture along the occipital margin. Vertex, especially towards the temples, predominantly scaly-reticulate ; the ocellar region is circumscribed, not very regularly, with a series of fine striations which are weaker on the vertex, where they break up into scaly-reticulate sculpture, but on the frons tend to change into fine, more or less longitudinal striation ; in small individuals, the surface of the head is more shining and the sculpture correspondingly weaker and more indefinite. Ocellar triangle, smooth, shining ; ocell-ocular line to distance between the posterior ocelli as 28 : 11. Antennae 29–33-segmented (two rather small ♀♀ ; antennae broken in larger individuals) ; flagellum 1 to 2 as 4 : 3.

Thorax : mesonotum falling rather steeply to pronotum, dull, clothed thickly with fine, very short, brownish hairs ; these hairs show no characteristic arrangement ; lobes of the mesonotum almost everywhere with a fine, close scaly-reticulate sculpture. Notauli somewhat fine, marked posteriorly by a fine ridge. Propodeum with two large, well defined, dorsal areas which are, in far greater part, dull, evenly scaly-reticulate ; posteriorly, the surface of these areas tends to become completely smooth and shining ; surface outside the areas reticulate-rugose. Mesopleurae with a sharply defined, crenate-rugose furrow ; surface of the mesopleurae immediately adjacent to the furrow, smooth and shining. Mesosternum shining, virtually smooth. Wings (fig. 2, **c**) : 2nd abscissa of the radius of the fore wing hardly one and a-half times as long as the 1st. Legs : hind tibiae without long hairs, those on the outer and upper side being only from one and a-half times to twice as long as those on the inner ; outer apical lobe of the hind tibia with a row of spines ; segment 1 of the hind tarsus about two and a-half times as long as 2, 26 : 11 ; hind coxa with a small projection beneath at base. *Abdomen* with 6 visible tergites (tergite (2+3) being reckoned as 2) each of which is sharply margined laterally (fig. 3, **a**). Petiole only very slightly longer than its apical width, 21 : 19, though appearing longer, finely, closely and fairly evenly striate, the surface between the ridges crenate. Tergite (2+3) slightly longer than its basal width, 8 : 7, provided with 2 costate furrows which converge laterally and enclose a transverse, fusiform area ; the segment is thus divided into 3 areas, which, measured medially, are more or less equal in length ; the basal area is wrinkly-striate, rugulose between the ridges ; the middle area is predominantly reticulate-rugose ; the apical area is evenly, longitudinally striate, the ridges fading out before apex ; their interstices are virtually smooth. Tergites 4 and 5 each with a transverse furrow (often concealed) at base ; the surface basal to the furrow is scaly-reticulate ; apical to it, like that of the apical area of tergite (2+3) ; tergite 5 has a broader smooth apical margin than 4 and in this respect is like 6. Apical margin of 6 straight, in profile (*cf. R. cleanthes*, sp. n., fig. 3, **c**). Ovipositor sheaths about two-thirds as long as abdominal tergites 1–6 together.

Length : 3–3·3 mm. (without ovipositor).

♂. More slender than the female and less dark in colour, being usually reddish-brown throughout ; sometimes the lobes of the mesonotum are darkened ; in two examples, the head and thorax are predominantly dark brown as in the female. Apex of abdomen apparently not hidden by tergite 6 as in the female ; sculpture of abdomen as in female, but weaker.

Length : 2·8–3·2 mm.

South India : Coimbatore, 20.vi.1936, 3 ♀♀, 2 ♂♂, bred from *Lixus* sp. ; 31.xii.1935, 1 ♀, bred from *Lixus* sp. ; viii–x.1937, 8 ♂♂, bred from *Pempheres affinis*, Fst., in

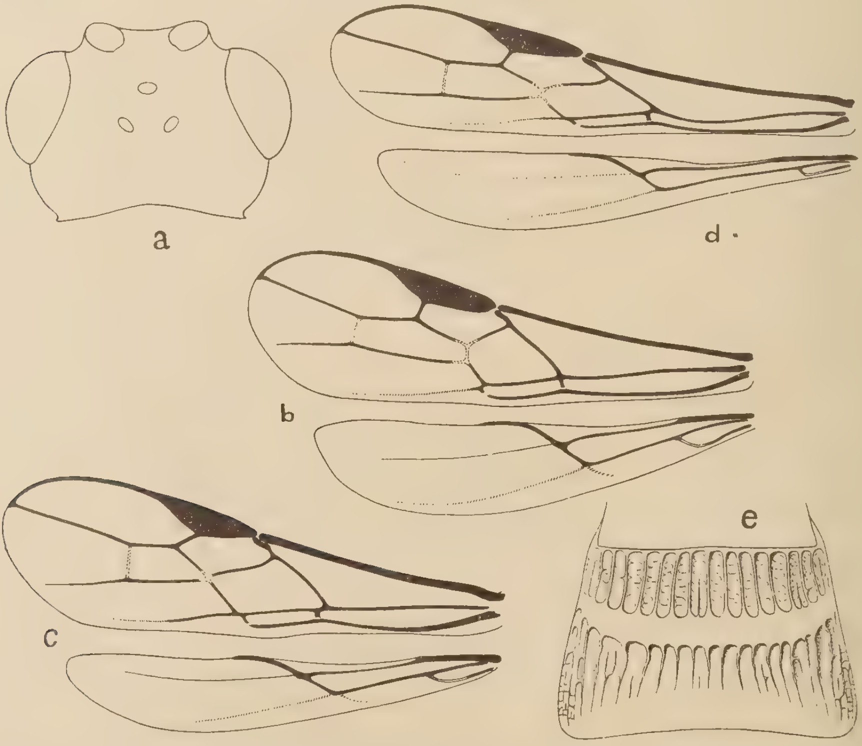

Fig. 2. **a,** *Rhaconotus menippus*, sp. n., ♀, head (from above) ; **b,** *Spathius critolaus*, sp. n., ♀, wings ; **c,** *Rhaconotus menippus*, sp. n., ♀, wings ; **d,** *Rhaconotus cleanthes*, sp. n., ♀, wings ; **e,** *Rhaconotus signipennis* (Walker), ♀, tergite (2+3).

Corchorus olitorius ; 26.i.1938, 1 ♀, bred from *Pempheres affinis* in cotton ; 25.vi.1938, 1 ♀, *the type*, bred from *Pempheres affinis* in *Triumfetta rhomboidea* ; 8.iii.1938, 1 ♂, bred from *Hypolixus truncatulus*, F., in *Amaranthus*.

This species is characterised by the division of tergite (2+3) into three areas and by having the middle one of these areas differently sculptured from the other two. The fine striation surrounding the ocelli is also likely to be specific.

Rhaconotus menippus var. **africana** var. n.

The material to which I have given this name consists of a large number of females from South Africa. The only differences I can find between them and typical *menippus* females are as follows :—

Ocelli not circumscribed so distinctly by fine striation ; the vertex, in consequence, more evenly and extensively scaly-reticulate. The head itself slightly less transverse than in *menippus*. Sculpture of middle area of tergite (2+3) contrasting less with that of the basal and apical areas ; this is due to a longitudinal element in the sculpture being more in evidence.

None of the above differences, either singly or in combination, seems to me to be sufficiently characteristic to have specific value. But they do justify, I think, a varietal name.

CAPE PROVINCE ; Somerset East, Sept.–Jan. (majority in September), 33 ♀♀ (*R. E. Turner*).

Rhaconotus cleanthes, sp. n.

♀. Deep reddish-brown ; darker in large individuals, paler and more evenly coloured in smaller. Head unicolorous, reddish-brown in all individuals. Antennae on basal half coloured like the head, darkened towards apex. Fore wings darkened ; an ill-defined hyaline patch in the radial cell and an irregular hyaline fascia crossing the wing and cutting off basal third of stigma. Legs more or less unicolorous, always paler than the body but more or less the same colour ; the coxae tend to be darker than the other parts.

Head transverse, clearly narrower behind the eyes than across them but less so than in *menippus*, sp. n. (*cf.* fig. 2, **a**) ; clothed above only with a few short, adpressed hairs and appearing virtually glabrous here. Face clothed with the usual hairs, dull, almost scabrous, with hardly a trace of transverse elements in the sculpture (× 40). Vertex extremely finely and, for the most part, evenly reticulated, the lines forming the meshes distinctly raised (for this reason, I do not use the term " scaly-reticulate," though the sculpture could, at first sight, be so described) ; this sculpture extends downwards over the temples and covers the cheeks but loses its sharpness and tends to become broken up into a vague surface-sculpture. Frons sculptured much like the vertex but the reticulations tend to form lines. Ocelli arranged in an equilateral triangle ; ocell-ocular line about 3·5 times as long as the distance between the posterior ocelli. Antennae with 32–39 segments (4 ♀♀) ; flagellum 1 very slightly longer than 2, 9 : 8. *Thorax* : mesonotum sloping somewhat gradually to pronotum, bare except for sparse, short, almost adpressed, pale, thick hairs which margin the rather wide notauli ; its sculpture consists predominantly of fine, somewhat broken scaly-reticulation. Propodeum without a trace of the delimited areas such as occur in *menippus*, sp. n. ; an obsolete, medial keel is present and two similar, lateral ones, between which lie the spiracles ; apart from these five ridges, the propodeum usually shows others, shorter, less well defined, subconfluent ; the whole surface of the sclerite, including that of the ridges, is covered with a glistening, feeble scaly-reticulation. Metapleurae not in any way differentiated from the propodeum, similarly sculptured and provided with three longitudinal keels, which, in small individuals, tend to be confluent. Mesopleurae with a well defined, feebly crenate furrow ; above the furrow, feebly shining, somewhat vaguely scaly-reticulate. Mesosternum more shining than the mesopleurae, its sculpture extremely feeble, sometimes almost absent. Wings (fig. 2, **d**) : medius of the fore wing taking a deep, downward curve before reaching the basalis ; 2nd abscissa of the radius at least 2·5 times as long as the 1st and distinctly longer than the 1st transverse cubitus. Legs : hind coxae with a projection beneath at base ; hind tibiae with long, very sparse, outstanding hairs, almost twice as long as the width of the tibia, on the *outer* side, not outer and upper sides, as in the case of species of *Doryctes*, Hal., when they have similar hairs ; segment 1 of the hind tarsus a little more than twice as long as 2, 5 : 4 ; outer, apical lobe of the hind tibia without differentiated spines. *Abdomen* with 5 visible tergites (fig. 3, **d**). Petiole gradually widened from base to apex, 1·5 times as long as its apical width, extremely finely reticulate and with scattered, feeble, much broken wrinkles ; in small individuals, these longitudinal elements tend to disappear completely. Tergite (2+3) with a broad furrow a little beyond middle, its ground sculpture like that of the petiole but otherwise with longitudinal striation much more in evidence ; basal to furrow, feeble, broken wrinkles are present but apical to furrow, the wrinkles are less broken and straighter ; this difference is not always well marked. Sculpture of tergite 4 beyond the basal furrow, which is almost hidden, like that of the apex of tergite (2+3). Tergite 5 large, finely and evenly reticulated right up to apex ; the base of the cells appears flat and shining ; apical margin of this tergite, seen in profile, distinctly emarginate (fig. 3, **c**). Tergites 1, (2+3) and to a less extent 4 carinate laterally above the spiracles, a lateral margin being delimited which lies more or less at right angles to the dorsal surface of the tergites and which, in the case of tergite (2+3) and 4, is virtually without longitudinal sculpture. Ovipositor sheaths about half as long as tergites 1–5 together.

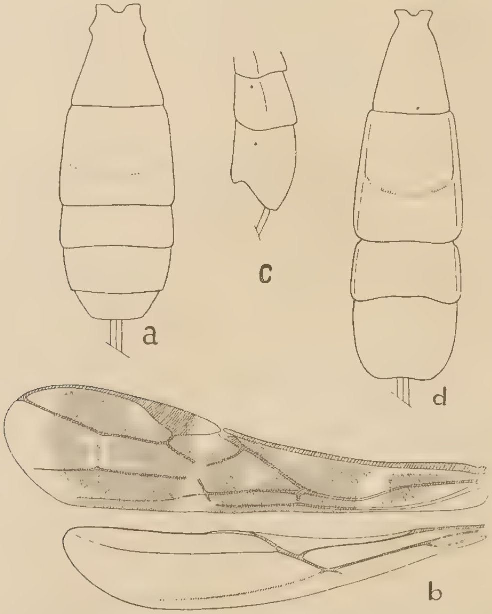

Fig. 3. **a,** *Rhaconotus menippus*, sp. n., ♀, abdomen (dorsal) ; **b,** *Spathius labdacus*, sp. n., ♀, wings ; **c,** *Rhaconotus cleanthes*, sp. n., ♀, apical tergites (lateral) ; **d,** *R. cleanthes*, sp. n., ♀, abdomen (dorsal).

Length: 2·4–3·7 mm. (without ovipositor); type ♀, 3·4 (without ovipositor).

♂. Antennae with 30–32 segments (2 ♂♂). Abdomen with 5 visible tergites, the 5th longer than the 4th as in the female and concealing the apical tergites, its apical margin, in profile, not emarginate.

Length: 2·9 mm. approx.

South India: Coimbatore, bred from *Pempheres affinis*, Fst., as follows: 29.x.1937, 2 ♀♀, host in *Triumfetta rhomboidea*; Coimbatore, Dhone, 1.x.1937, 2♀♀, 1 ♂, host on *Sida acuta*; Kuniamuthur, 25.vi.1938, 1 ♂, 3 ♀♀ (one *the type*), host in *Triumfetta rhomboidea* (*P. N. Krishna Ayyar*).

This species clearly belongs to a different species-group, if not genus, from *R. menippus*, sp. n. Probably characteristic for the group are:—Darkened fore wings with their hyaline markings, curvature of medius of fore wing, sculpture of propodeum, especially in regard to its lack of delimited dorsal areas, and arrangement of hairs on the hind tibiae.

Specifically, *R. cleanthes*, sp. n., is largely characterised by the sculpture of the abdomen, particularly of tergite 5.

Rhaconotus signipennis (Walker) (new combination).

Spathius signipennis, Walk., 1860, Ann. Mag. Nat. Hist. **5**, p. 309, ♀; Szepligeti, 1905, Gen. Ins. (Braconidae), p. 53.

Stenophasmus signipennis (Walker), Enderlein, 1912, Arch. für Naturges. A (2), p. 11.

This species, of which the type is in the British Museum, belongs, in my opinion, to the group of *menippus*, sp. n., though it differs from that species strikingly in the sculpture of the abdomen. It may be compared with *menippus* as follows:—

♀. Paler in colour; the type is unicolorous reddish-brown, except for the head which is yellowish; the legs are unicolorous pale yellow. In examples from Dehra Dun, the mesonotum is pale brownish-red or brownish-yellow and contrasts rather sharply with the blackish propodeum; abdomen reddish with lighter and darker suffusions; the largest ♀ (Dehra Dun, 22.iv.1930, *J.C.M.G.*) has a conspicuous yellowish spot on each side of tergites (2+3)–5; in small individuals, the colour tends to become uniform reddish-yellow; in all the N. India specimens, the legs are very pale yellow like those of the type. In the type, the stigma is more yellow and the veins darker than in the N. India material.

Head less transverse than in *menippus*, the eyes less prominent; hence the head behind the eyes less narrowed (*cf.* fig. 2, **a**). Vertex and frons evenly scaly-reticulate all over, without a trace of raised sculpture (striation). Antennae with 21–28 segments (25 in type). *Thorax*: fine pubescence of mesonotum whitish. Mesopleural furrow smooth, except perhaps for a trace of the scaly-reticulation which covers the greater surface of the mesopleurae; the furrow is deepest and widest posteriorly. Legs: hairs of the outer side of the hind tibia longer than in *menippus*; in a dorsal view of the tibia, the outer hairs are about as long as the width of the tibia and nearly three times as long as those on the inner side. *Abdomen*: 6 tergites visible (tergite (2+3) being reckoned as 2) as in *menippus*. Petiole almost exactly as long as apically wide, its ridges less close than in *menippus*, their interstices more noticeably sculptured. Tergite (2+3) with a medial, transverse, smooth, unsculptured band (fig. 2, **e**); this band is bounded basally by a sculptured area and apically by a costate furrow from which extends fine striation; this striation does not reach the apex of the segment; the interstices of the ridges of the basal area are much sculptured. Tergites 4 and 5 with a furrow at base (generally concealed), from which arises striation similar to that of the apical part of tergite (2+3). The declivous sides of tergites (2+3)–5 are almost rugose-striate. Tergite 6 larger and more sculptured than in *menippus*, showing coarse, more or less concentric striation, which runs more or less parallel to the curve of the apical margin ; in small examples, the striation is almost wanting, the surface becoming smooth except for a lateral patch of sculpture similar to that on the declivous, lateral face of tergite 5. Ovipositor sheaths less than half the length of tergites 1–6 together.

Length : 1·8–3·1 mm. (without ovipositor).

♂. Abdomen long and narrow. Basal, sculptured area of tergite (2+3) much less transverse than in ♀ and the smooth, medial band much narrower. Apical part of tergite (2+3) and of tergites 4–6 less smoothly striated. Basal furrow of tergites 4 and 5 deeper than in the ♀.

Length : 2·2 mm. approx.

CEYLON : (Type ♀). UNITED PROVINCES : Dehra Dun, Jhajra, 5.iv.1929, 3 ♀♀ (*J. C. M. Gardner*) ; Dehra Dun, 27.iv.1930, 3 ♀♀, 1 ♂, bred from dry wood (*J.C.M.G*) ; Dehra Dun, Sherpur, 1.iv.1930, 1 ♂, 23.xii.1929, 1 ♂ (*B. S. Gusain*).

This species is chiefly characterised by the sculpture of tergite (2+3). I know of no other species of *Rhaconotus*, either described or undescribed, which is similarly sculptured.

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WILKINSON, D. S. (1927). Eight new species of Braconidae.—Bull. Ent. Res., **18,** pp. 33–46.

——. (1929). New species and host records of Braconidae.—Bull. Ent. Res., **20,** pp. 205–208.

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KEYS TO THE KNOWN LARVAE AND ADULTS OF WEST AFRICAN ANOPHELINE MOSQUITOES.

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These keys and illustrations have been prepared in response to many requests. They concern only those species of *Anopheles* which have been recorded as occurring in West Africa south of the Sahara Desert as far as the equator. Much of the material has been derived from the recent Monograph by the late Dr. A. M. Evans on the Anophelines of the Ethiopian Region published by the British Museum in 1938. Personal acquaintance with the Anophelines of East and South Africa and examination of the specimens in the collection of the Department of Entomology of the London School of Hygiene and Tropical Medicine have assisted in the preparation of the keys.

No general descriptions of mosquito anatomy are considered necessary, as the keys are intended for use by those having this elementary knowledge. The illustrations are essentially diagrammatic and not in any sense drawn to scale. In the abbreviated descriptions the dark areas (first to fourth) on the wings include both the costa and the first vein, so that where a part of any particular dark area is interrupted or unlike that of its corresponding part on the costa or on the first vein the irregularity is indicated.

Two of the species are unknown in the larval stage, *A. wellcomei* and *A. flavicosta.* No drawings have been made of the adult and larval characters of *A. obscurus* or the larval characters of *A. hargreavesi*, as the descriptions are self-explanatory.

The adult keys and descriptions are based mainly on females, the larval keys entirely on fourth stage characters.

The Anopheline should first be run down by means of the key and then the identification checked by consulting the short description of the species, together with the accompanying illustration.

Key to Species of West African Anopheline Mosquitoes.

Adults.

(Based mainly on females.)

1. Abdominal segments with laterally projecting tufts of scales........................7
   Abdominal segments without laterally projecting tufts of scales.................2
2. Hind tarsi with at least 2 segments entirely pale.....................................3
   Hind tarsi with last 2 segments not entirely pale.....................................9
3. Legs speckled...4
   Legs not speckled...5
4. ♀ palpi speckled ; last 3 segments of hind tarsi entirely pale........................ *maculipalpis* (p. 142)
   ♀ palpi not speckled ; last 2 segments only of hind tarsi entirely pale........... *pretoriensis* (p. 142)
5. ♀ palpi very shaggy, with pale bands narrow, usually 4 but may be reduced to 2 or 3..*paludis, coustani* and vars. (p. 131)
   ♀ palpi not shaggy, with 3 pale bands, the 2 outer ones broad.....................6
6. Mesonotal scales broad ; third main dark area on vein 1 not interrupted by pale spot..*rufipes* and var. *ingrami* (p. 141)

Mesonotal scales almost entirely very narrow ; third main dark area on vein 1 interrupted by pale spot..........*hancocki* (p. 138)

7. Hind tarsi with last segment entirely dark ; pale bands at apices of most segments..........*squamosus* (p. 144)

Hind tarsi with last segment not entirely dark..........8

8. Last segment of fore- and mid-tarsi entirely dark ; pale grey mosquito..........*pharoensis* (p. 143)

Last segment of fore- and mid-tarsi entirely pale ; yellowish rings on legs ; very small species, not pale grey..........*cinctus* (p. 132)

9. Legs speckled ; ♀ palpi with 3 pale bands, the apical one broad..........*gambiae* (*costalis*) (p. 140)

Legs not speckled..........10

10. ♀ palpi shaggy and entirely dark..........*obscurus* (p. 131)

♀ palpi not shaggy and with 1 or more pale bands..........11

11. ♀ palpi with 1 pale band only, at apex..........*nili* (p. 133)

♀ palpi with more than 1 pale band..........12

12. ♀ palpi with 3 obscure pale bands ; apex dark ; pale spots on wings greatly reduced in ♀..........*smithi* (p. 132)

♀ palpi with apex pale and 2 other pale bands..........13

13. Wings with pale spots confined to costal region..........*rhodesiensis* (p. 139)

Wings with pale spots on other veins also..........14

14. Outer half of proboscis clothed with pale scales ; wing field abnormally pale *wellcomei* (p. 139)

Outer half of proboscis dark..........15

15. Wings with pale interruption in third main dark area on vein 1..........*hargreavesi* (p. 135)

Wings without pale interruption in third main dark area on vein 1..........16

16. Costa with 1 or 2 pale interruptions in basal quarter..........17

Costa without pale interruption in basal quarter......*funestus* (atypical) (p. 134)

17. ♀ palpi with subapical pale band narrow..........*funestus* (typical) (p. 134)

♀ palpi with the 2 distal pale bands broad..........18

18. Hind tarsi without definite pale rings or bands..........19

Hind tarsi with definite pale rings or bands..........20

19. Small species (wing length about 2·4–3·3 mm.) ; on ♀ palpi intervening dark band between distal pale bands usually wider than either pale band..........*funestus* (atypical) (p. 134)

Larger species (wing length about 3·5–4·5 mm.) ; on ♀ palpi dark band between distal pale bands narrower than either pale band......*freetownensis* (p. 140)

20. Costa mainly yellow on outer half..........*flavicosta* (p. 136)

Costa not so..........21

21. Hind tarsi without any pale scales at *bases* of segments..........*moucheti* var. *nigeriensis* (p. 134)

Hind tarsi with pale scales at base of at least 1 segment..........22

22. Hind tarsi with pale rings extending well on to bases of most of the segments *domicolus* (p. 137)

Hind tarsi with pale rings extending at most slightly on to the bases of the segments..........*barberellus* (p. 137)

Anopheles coustani, Laveran (fig. 1).

PALPS.—Shaggy ; four narrow pale bands (one at apex) sometimes hardly perceptible.

MESONOTUM.—Bristles and hairs.

HIND TIBIAE.—Large pale apical patch, four times width of tibia.

HIND TARSI.—I, broad pale ring at base and apex ; II, apical third or more pale ; III, apical two-thirds pale ; IV & V, entirely pale.

WINGS.—*Costa.* Two pale spots.
3rd vein. Usually mainly dark.
5th vein. Stem and lower branch pale at bifurcation.
Apex. Small pale spot not reaching to 3rd vein.
Fringe. Entirely dark.

ABDOMEN.—Ventral surface, tuft of dark scales on 7th sternite.

NOTES.—(*a*) Common variations in West African specimens :
Hind tarsi (fig. 1, A). I, apical pale ring narrow ; III, entirely pale.

(*b*) Var. *ziemanni*, Grünberg, differs from type form as follows :—
Hind tibiae. Pale apical patch small.
Wing. Pale apical fringe spot large, extending to 3rd vein.

(*c*) *A. paludis*, Theobald, differs from *A. coustani* as follows :—
Hind tibiae. Pale apical patch reduced to very small spot.
Hind tarsi. I, base dark ; III, entirely pale.
Wing. Pale apical fringe spot large, extending to 3rd vein ; pale fringe spot opposite vein 5·2.

(*d*) Species and varieties rare in houses and of no practical importance as vectors of malaria.

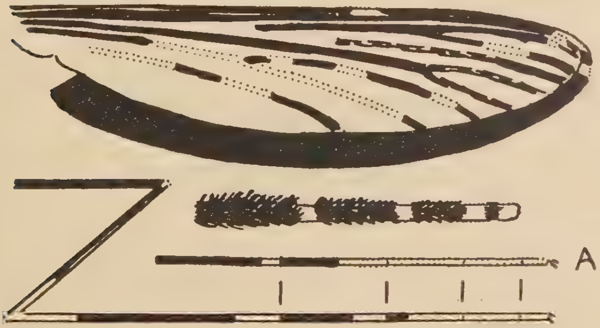

Fig. 1. *Anopheles coustani*, Laveran.

Anopheles obscurus, Grünberg.

PALPI.—Shaggy ; entirely dark.

MESONOTUM.—Bristles, short brassy hairs.

HIND TARSI.—I–IV, narrow pale apical rings ; V, entirely dark.

WINGS.—*Costa* with two minute pale spots, one near apex.
Other veins variable, general effect dark.
Apex. Dark.
Fringe. Mainly dark ; pale spot between veins 3 and 4·1.

ABDOMEN.—Hairs.

NOTES.—(*a*) Var. *nowlini*, Evans, differs mainly from the type form in having the " wings constantly with 2–6 small, pale spots on about the basal half of the first vein " (Evans, 1938).

(*b*) Rare in houses and evidently of little importance as a vector of malaria.

Anopheles cinctus, Newstead & Carter (fig. 2).

PALPI.—Shaggy ; four narrow white bands (one at apex).

MESONOTUM.—Anterior, broad flat whitish scales ; posterior, narrow curved.

FEMORA AND TIBIAE.—Spotted and ringed with yellowish scales.

HIND TARSI.—Remarkably regular alternation of pale and dark rings.

WINGS.—*1st dark area.* Two pale interruptions on costa and on vein 1.

2nd dark area. One pale sub-basal interruption on 1st vein.

3rd dark area. Uninterrupted.

3rd vein. Extensively pale with one dark apical spot and sometimes one or two basal ones.

5th vein.—Stem and lower branch pale at bifurcation.

Apex. Dark spot.

Pale fringe spots. Opposite ends of veins and sometimes another basally.

ABDOMEN.—Some pale scales on dorsal surface ; II–VI, lateral tufts of dark scales ; VIII, dark scales confined to small lateral spots.

NOTE.—Localized jungle species of no importance as malaria vector.

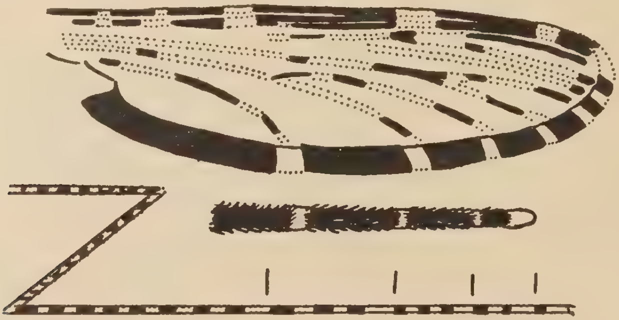

Fig. 2. *Anopheles cinctus*, Newstead & Carter.

Anopheles smithi, Theobald (fig. 3).

PALPI.—Smooth ; three pale, rather dusky bands ; apex usually dark.

MESONOTUM.—Hairs.

HIND TARSI.—Entirely dark.

WINGS.—Very dark ; pale spots minute, obscure, sometimes absent.

Apex. Dark.

Fringe. Entirely dark.

ABDOMEN.—Blackish, very dark bristles.

Cerci. Numerous scales.

NOTES.—(*a*) In the ♂ wing typical specimens show four well-marked pale costal spots and other pale spots at bases of fork-cells and near cross-veins. Other pale spots may be present. Any of these pale spots may be reduced or absent.

(*b*) Rare in houses except near breeding places ; otherwise of little importance as malaria vector.

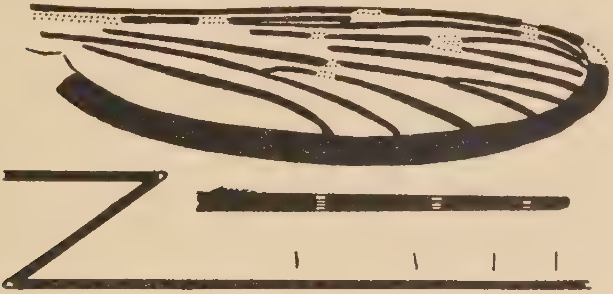

Fig. 3. *Anopheles smithi*, Theobald.

Anopheles nili, Theobald (fig. 4).

PALPI.—Smooth ; one pale band at apex only.

MESONOTUM.—Dark bristles, pale hairs.

FEMORA AND TIBIAE may have very faint apical pale bands.

HIND TARSI.—Entirely dark.

WINGS.—*1st dark area.* Entirely dark on costa (may be a small pale interruption) ; 1st vein, pale interruption midway.

2nd dark area. On first vein may be shorter basally than dark area on costa.

3rd dark area. Uninterrupted.

3rd vein. Entirely dark.

5th vein. Dark or pale at bifurcation.

Apex. At end of vein 2·1 pale spot ; at end of vein 2·2 dark spot.

Pale fringe spots. Opposite veins 4·2 and 5·2 ; may be others also but never opposite vein 6.

ABDOMEN.—Hairs.

NOTE.—Rare in houses. If prevalent in native dwellings may be of importance as malaria vector. Has been found infected with filaria.

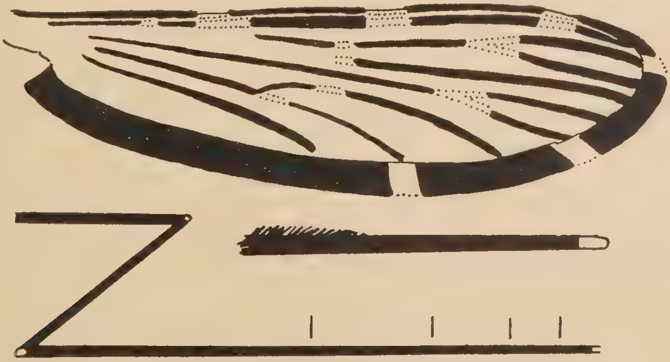

Fig. 4. *Anopheles nili*, Theobald.

Anopheles funestus, Giles (fig. 5).

PALPI.—Smooth ; three pale bands including apex, variable in width but commonly relatively narrow ; intervening dark band may be equal to but is usually wider than either distal pale band.

MESONOTUM.—Hairs or hair-like scales.

HIND TARSI.—Entirely dark, but may have obscure pale rings at apices.

WINGS.—1*st dark area.* Interrupted by one pale spot on costa or uninterrupted on costa ; base of vein 1 pale.

2*nd dark area.* Shorter basally on vein 1 than on costa.

3*rd dark area.* Uninterrupted.

3*rd vein.* (a) Usually pale beyond middle with dark spots at each end, basal dark spot being larger ; (b) may be entirely dark.

5*th vein.* Dark at bifurcation.

Apex. One or two dark spots.

Pale fringe spots. Present, except opposite vein 6.

ABDOMEN.—Hairs.

NOTES.—(*a*) In ♂ palp there is no pale spot at base of club.

(*b*) Varieties of *A. funestus* so far not recorded from W. Africa : v. *confusus,* Evans & Leeson, and v. *fuscivenosus,* Leeson.

(*c*) Species closely related to *A. funestus* but so far not recorded from W. Africa : *A. rivulorum,* Leeson, and its variety v. *garnhamellus,* Evans & Leeson, and *A. leesoni,* Evans.

(*d*) Type form common in houses, often with *A. gambiae.* Other forms not house-frequenting in S. and E. Africa. *A. funestus* and *A. gambiae* are the most important malaria vectors in the Ethiopian region.

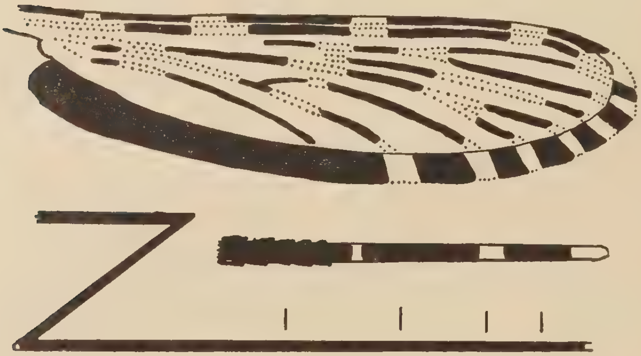

Fig. 5. *Anopheles funestus,* Giles.

Anopheles moucheti var. **nigeriensis,** Evans (fig. 6).

PALPI.—Smooth ; three pale bands, two distal ones broad ; intervening dark bands narrower than either pale band and sometimes absent.

MESONOTUM.—Scales, narrow to very narrow.

LEGS.—Unspeckled, pale knee spots on tibiae.

HIND TARSI.—I–IV, pale apical rings ; V, entirely dark.

WINGS.—1*st dark area.* One or two pale interruptions on costa ; basal portion of vein 1 pale.

2nd dark area. One pale sub-basal interruption on 1st vein.

3rd dark area. No interruption.

3rd vein. One apical and one sub-basal small dark spot.

5th vein. Dark spot at bifurcation.

Apex. Dark spot.

Pale fringe spots. Present except at end of 6th vein.

ABDOMEN.—Hairs.

NOTES.—(*a*) The type form has not been reported from W. Africa ; it has some broad scales on the mesonotum.

(*b*) The variety frequents native huts and may be an important malaria vector where it is found in large numbers.

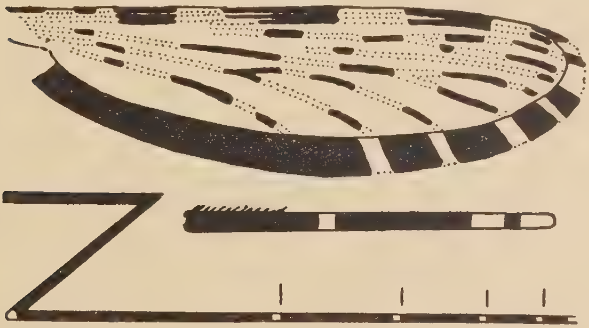

Fig. 6. *Anopheles moucheti* var. *nigeriensis*, Evans.

Anopheles hargreavesi, Evans (fig. 7).

PALPI.—Smooth ; three pale bands including apex ; intervening dark band narrower than either distal pale band.

MESONOTUM.—Broad greyish white scales.

HIND TARSI.—I–IV, narrow pale apical rings ; V, entirely dark.

WINGS.—1*st dark area.* Often with two pale interruptions on costa ; basal portion vein 1 pale.

2nd dark area. One pale sub-basal interruption on 1st vein.

3rd dark area. Pale interruption midway on 1st vein.

3rd vein. Pale with one dark apical and one or two dark basal spots.

5th vein. Dark at bifurcation.

Apex. Small dark spot.

Pale fringe spots. Opposite vein ends (small at 6th).

Abdomen.—Hairs.

Note.—Frequents native dwellings and probably of some importance as a malaria vector.

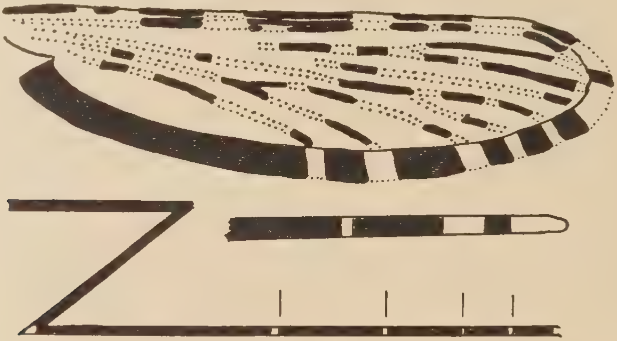

Fig. 7. *Anopheles hargreavesi*, Evans.

Anopheles flavicosta, Edwards (fig. 8).

Palpi.—Smooth ; three pale bands including apex, two distal ones broad ; intervening dark band narrower than either distal pale band.

Mesonotum.—White, narrow curved scales.

Hind Tarsi.—I–IV, distinct pale apical bands ; V, entirely dark.

Wings.—Scales mainly yellow, dark spots reduced.

1st dark area. Interrupted on costa by one or two pale spots; base of 1st vein extensively pale.

2nd dark area. Basal third pale on 1st vein.

3rd dark area. Reduced, uninterrupted.

4th dark area. Very small.

3rd vein. Two small dark spots near base ; may be one near apex.

5th vein. Small dark spot at bifurcation.

Apex. Extensively pale, reaching to 3rd vein (may be one small dark interruption).

Pale fringe spots. Opposite veins 4 to 6.

Abdomen.—Golden yellow hairs.

Note.—Rare in houses. No practical importance as a malaria vector.

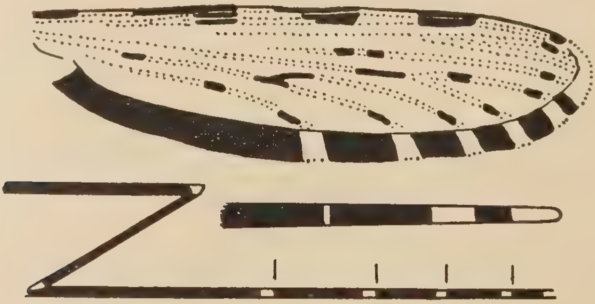

Fig. 8. *Anopheles flavicosta*, Edwards.

Anopheles domicolus, Edwards (fig. 9).

PALPI.—Smooth ; three pale bands, two distal ones very broad ; intervening dark band much shorter than either distal pale band.

MESONOTUM.—Very narrow curved white scales, broader towards front.

HIND TARSI.—Broad pale rings at articulations involving apices of I–IV and bases of II–V.

WINGS.—1*st dark area.* One pale interruption on costa ; base of vein 1 pale.

2*nd dark area.* One pale sub-basal interruption on 1st vein.

3*rd dark area.* No interruption.

3*rd vein.* Pale with one dark apical spot and one or two dark spots basally.

5*th vein.* Dark spot at bifurcation.

Apex. Small dark spot.

Pale fringe spots. Present except opposite 6th vein.

ABDOMEN.—Hairs.

NOTE.—Uncommon. No practical importance as malaria vector.

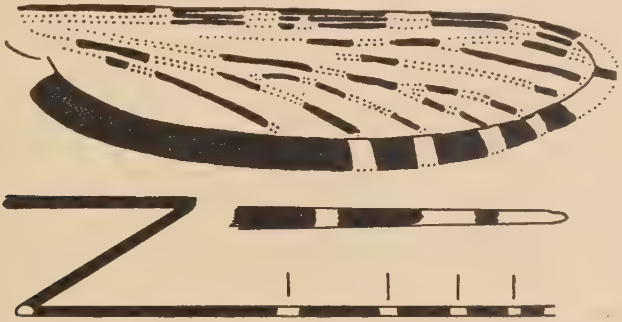

Fig. 9. *Anopheles domicolus,* Edwards.

Anopheles barberellus, Evans (fig. 10).

PALPI.—Smooth ; three pale bands, two distal ones broad ; intervening dark band narrower than either distal pale band.

MESONOTUM.—Narrow whitish scales, broader in front.

HIND TARSI.—I–IV, pale apical rings ; IV–V, very narrow pale basal rings.

WINGS.—1*st dark area.* Interrupted by two large, pale spots on costa ; base of costa sometimes pale ; base of vein 1 pale.

2*nd dark area.* Sometimes with pale interruption on costa ; one large sub-basal pale interruption on 1st vein.

3*rd dark area.* Small, uninterrupted.

3*rd vein.* Pale, with one dark spot apically and one or two basally.

5*th vein.* Dark spot at bifurcation.

Apex. Dark spot.

Pale fringe spots. Present except opposite 6th vein.

NOTE.—Uncommon. No importance as malaria vector.

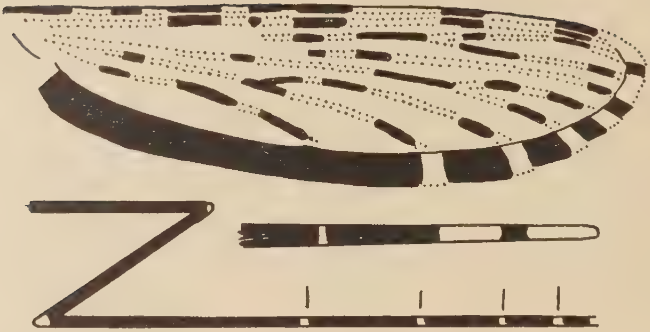

Fig. 10. *Anopheles barberellus*, Evans.

Anopheles hancocki, Edwards (fig. 11).

PALPI.—Smooth ; three pale bands, 2nd and 3rd broad, intervening dark band commonly narrower than either distal pale band.

MESONOTUM.—Narrow curved pale scales.

HIND TARSI.—I, usually entirely dark, may have pale apical ring ; II, pale apical ring ; III–V, entirely pale.

WINGS.—*1st dark area.* One or two pale interruptions ; base of 1st vein pale.

2nd dark area. One pale sub-basal interruption on 1st vein.

3rd dark area. Pale sub-basal interruption on 1st vein.

3rd vein. Pale with dark apical, basal and sub-basal spots.

5th vein. Dark spot at bifurcation.

Apex.—Dark spot.

Pale fringe spots.—Opposite ends of veins, sometimes not opposite 6th.

NOTE.—Frequents human dwellings. Not yet found to be a malaria vector in West Africa.

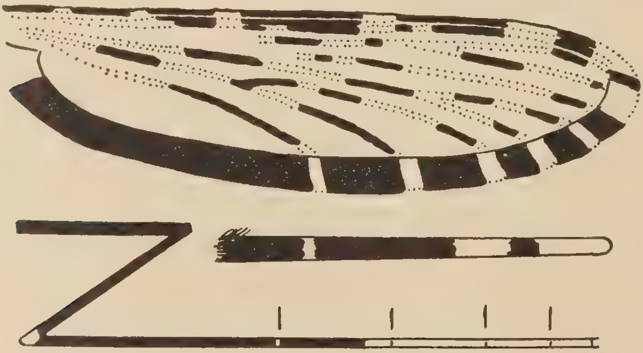

Fig. 11. *Anopheles hancocki*, Edwards.

Anopheles wellcomei, Theobald (fig. 12).

PALPI.—Smooth; basal third brown followed by a narrow white band, outer two-thirds yellow and white, the white scales forming two broad bands distally.

PROBOSCIS (fig. 12, A).—Outer half whitish or yellowish-white.

MESONOTUM.—Whitish or yellowish-white narrow curved scales.

LEGS.—Mainly dark brown.

HIND TARSI.—I–IV, distinct white apical rings; V, entirely dark.

WINGS.—Extensively pale.

Costa. Basal half dark; two other dark spots variable in size.

3rd vein. Almost entirely pale.

5th vein. Dark spot at bifurcation.

Apex. Extensively pale reaching to 3rd vein.

Pale fringe spots. Opposite veins 4, 5 & 6; sometimes a pale area in the basal portion.

ABDOMEN.—Pale yellow hairs.

NOTE.—In West Africa only recorded from Northern Nigeria. Probably unimportant as a malaria vector.

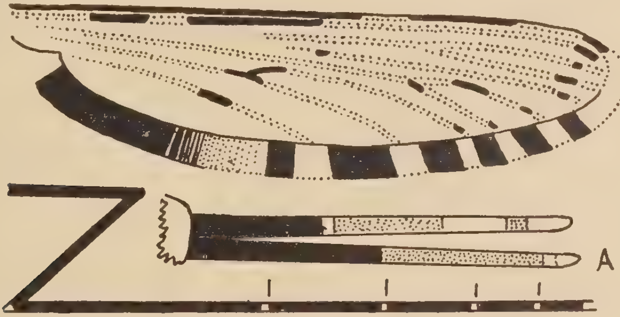

Fig. 12. *Anopheles wellcomei*, Theobald.

Anopheles rhodesiensis, Theobald (fig. 13).

PALPI.—Smooth; three pale bands which may be indistinct, especially the apical one; intervening dark band much wider than either distal pale band.

MESONOTUM.—Hairs.

HIND TARSI.—Entirely dark or with very faint apical pale bands.

WINGS.—*1st, 2nd, 3rd and 4th dark areas*: uninterrupted, but there may be a pale spot on vein 1 under 1st costal dark area; all other veins and fringe dark.

NOTE.—Not usually a house frequenter. Of little importance as a malaria vector.

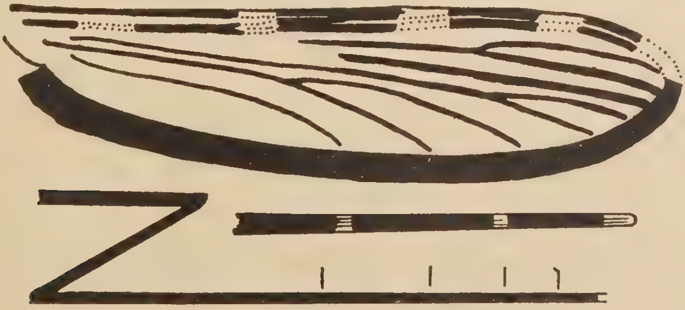

Fig. 13. *Anopheles rhodesiensis*, Theobald.

Anopheles freetownensis, Evans (fig. 14).

PALPI.—Smooth ; three pale bands including apex, two distal ones broad ; intervening dark band narrower than either distal pale band.

MESONOTUM.—Long narrow pale scales.

HIND TARSI.—Entirely dark.

WINGS.—1*st dark area.* Two pale interruptions on costa ; base of 1st vein pale.
2nd dark area. Shorter basally on 1st vein than on costa.
3rd dark area. Uninterrupted.
3rd vein. Large dark area near base ; smaller dark area near apex.
5th vein. Dark at bifurcation.
Apex. Small dark spot.
Pale fringe spots. Present except opposite 6th vein.

NOTE.—Not a house frequenter. No importance as malaria vector.

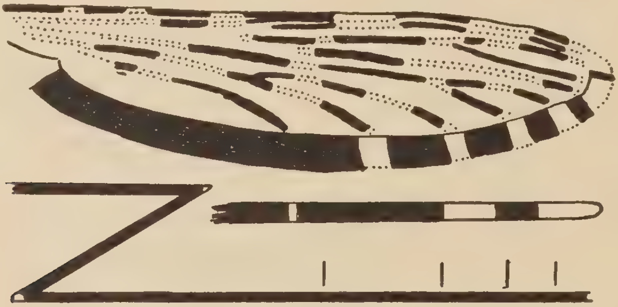

Fig. 14. *Anopheles freetownensis,* Evans.

Anopheles gambiae, Giles (fig. 15).

PALPI.—Smooth ; three pale bands including apex ; apical one broadest ; apical pale band may be divided into two by dark ring.

MESONOTUM.—Narrow pale scales.

FEMORA AND TIBIAE.—Speckled ; speckling may be inconspicuous.

HIND TARSI.—I–IV, pale apical rings ; V, entirely dark.

WINGS.—1*st dark area.* Two or three pale interruptions on costa ; base of first vein pale.
2nd dark area. Pale interruption sub-basally on 1st vein.
3rd dark area. Pale interruption on 1st vein.
3rd vein. Extensively pale, one dark spot apically and two basally.
5th vein. Pale at bifurcation.
Apex. Two small dark spots.
Pale fringe spots.—Opposite ends of veins ; sometimes one between vein 6 and vein 5·2 ; another in basal portion of fringe.

ABDOMEN.—Hairs.

NOTES.—(*a*) A melanic coastal form is widely distributed in West Africa ; the female palps have four pale bands and the pale areas on the wings may be reduced.

(*b*) A domestic Anopheline, in some places the only one, but in others with *A. funestus*. *A. gambiae* and *A. funestus* are the most important malaria vectors in the Ethiopian region.

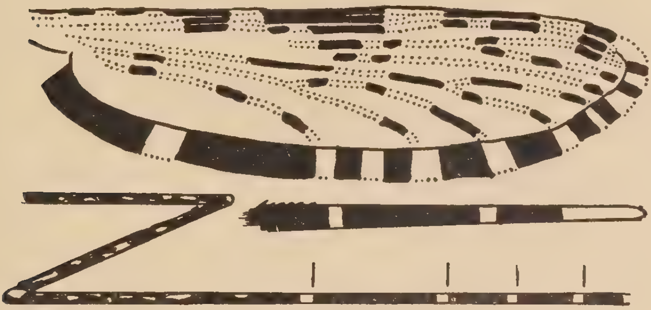

Fig. 15. *Anopheles gambiae*, Giles.

Anopheles rufipes, Gough (fig. 16).

PALPI.—Smooth ; three pale bands, including apex ; 2nd and 3rd broad. Intervening dark band often narrower than either distal pale band.

MESONOTUM.—Broad white scales.

HIND TARSI.—I and II, white-tipped ; III, about apical half white, sometimes narrow white ring at base ; IV and V, entirely white.

WINGS.—1*st dark area.* Interrupted by two pale spots on costa ; base of vein 1 pale.

2nd dark area. Two pale interruptions on vein 1.

3rd dark area. Uninterrupted.

3rd vein. Middle third usually pale ; vein may be entirely dark.

5th vein. Pale at bifurcation.

Apex. Dark spot.

Pale fringe spots. Opposite ends of veins.

ABDOMEN.—Hairs.

NOTES.—(*a*) Var. *ingrami*, Edwards (fig. 16, A) differs from the type form in having the third hind tarsal segment entirely white or with a narrow dark basal ring.

(*b*) Occasionally found in houses. No practical importance as malaria vector.

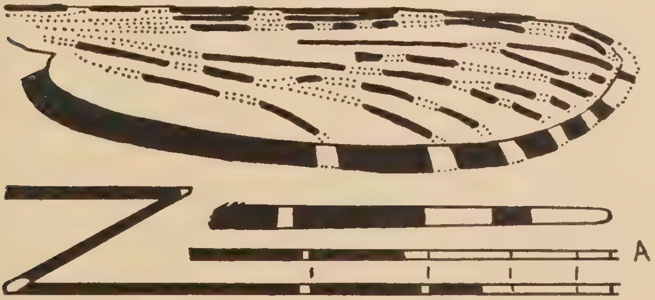

Fig. 16. *Anopheles rufipes*, Gough.

Anopheles pretoriensis, Theobald (fig. 17).

Palpi.—Smooth ; three pale bands, including apex ; 2nd and 3rd broad ; 2nd often narrower than indicated in figure ; 3rd may be divided into two by dark band.

Mesonotum.—Broad pale scales.

Femora, Tibiae and first segment of tarsi, pale speckling.

Hind Tarsi.—I and II, apices broadly pale ; III, distal half pale ; IV and V, entirely pale.

Wings.—*1st dark area.* Interrupted by two pale spots on costa ; 1st vein pale basally.

2nd dark area. Two pale interruptions on 1st vein.

3rd dark area. Uninterrupted.

3rd vein. Middle third usually pale ; vein may be entirely dark.

5th vein. Dark at bifurcation.

Apex. Dark spot.

Pale fringe spots. Opposite ends of veins.

Abdomen.—Hairs.

Note.—Rare in houses. No importance as malaria vector.

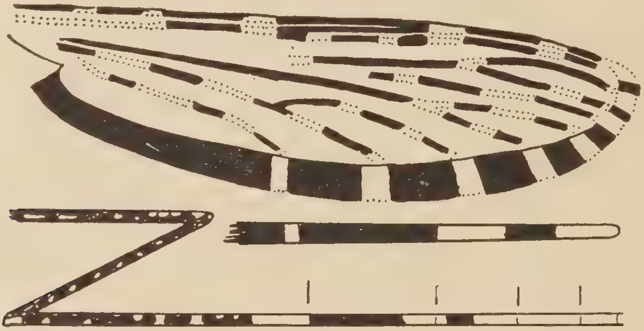

Fig. 17. *Anopheles pretoriensis,* Theobald.

Anopheles maculipalpis, Giles (fig. 18).

Palpi.—Smooth ; speckled with pale scales ; three pale bands including apex ; 2nd and 3rd broad ; width of intervening dark band usually equal to 3rd pale band.

Mesonotum.—Broad pale scales.

Femora, Tibiae and first segment of tarsi, speckled.

Hind Tarsi.—I, no pale speckling apically ; II, apical half pale ; III–V, entirely pale.

Wings.—*1st dark area.* Interrupted by two pale spots on costa ; base of 1st vein pale.

2nd dark area. Two pale spots on vein 1.

3rd dark area. Uninterrupted, joined to 2nd on vein 1.

3rd vein. Middle third, usually pale ; vein may be entirely dark.

5th vein. Dark or pale at bifurcation.

Apex. Dark spot.

Pale fringe spots. Opposite ends of veins.

ABDOMEN.—Hairs.

NOTE.—Not domestic. No importance as malaria vector.

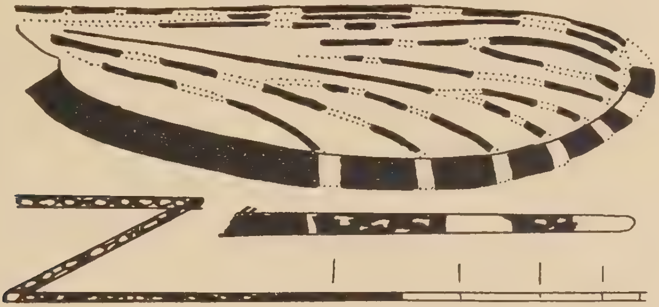

Fig. 18. *Anopheles maculipalpis*, Giles.

Anopheles pharoensis, Theobald (fig. 19).

PALPI.—Shaggy with pale scales among dark ones ; four pale bands including apex.

MESONOTUM.—Whitish broad scales ; two dark bare spots with stripes running back from them.

FEMORA AND TIBIAE.—Speckled.

HIND TARSI.—I–IV, broad pale apical bands ; V, entirely pale ; I, pale stripe (variable) ; IV, pale at base (variable).

WINGS.—Base of costa pale.

1*st dark area.* Considerably reduced, especially on 1st vein, where it may be represented by a small spot.

2*nd dark area.* One or more pale interruptions on 1st vein.

3*rd dark area.* One or more pale interruptions on 1st vein.

3*rd vein.* Extensively pale ; one dark apical spot and one or two basal ones.

5*th vein.* Dark spot present or absent at bifurcation.

Apex. Mainly pale.

Pale fringe spots. Opposite ends of veins and sometimes one in basal portion.

ABDOMEN (fig. 19, A).—Dense pale scales above ; laterally projecting tufts of dark scales.

Note.—Not common in human dwellings. Has been found naturally infected with sporozoites in West Africa but is probably of little practical importance as a malaria vector unless abundant.

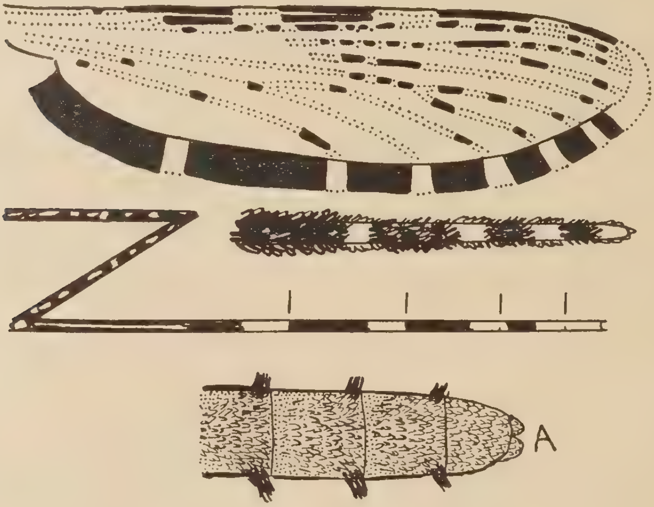

Fig. 19. *Anopheles pharoensis*, Theobald.

Anopheles squamosus, Theobald (fig. 20).

Palpi.—Shaggy; four variable pale bands including apex, apical pale band alone is distinct; may be some speckling.

Mesonotum.—Pale wide scales.

Femora and Tibiae.—Speckled.

Hind Tarsi.—I–IV, broad apical pale bands; I, irregular pale stripe; V, entirely dark.

Wings.—1*st dark area.* Variable number of pale interruptions on costa and 1st vein.

2*nd dark area.* Sub-basal pale interruption on 1st vein (variable).

3*rd dark area.* Sub-apical pale interruption on 1st vein (variable).

3*rd vein.* Pale area middle third (variable).

5*th vein.* Dark spot at bifurcation (normal).

Apex. Dark spot.

Fringe. Entirely dark or with pale spots opposite ends of veins.

Abdomen.—Laterally projecting tufts of dark scales; dark and pale scales on dorsal surface.

NOTE.—Not a common house-frequenter. Of no importance as a malaria vector.

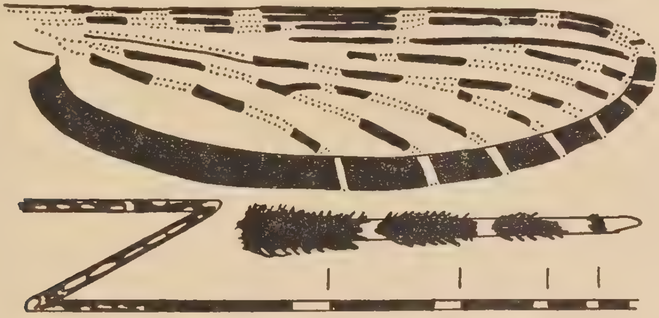

Fig. 20. *Anopheles squamosus*, Theobald.

Key to Species of West African Anopheline Mosquitoes.
Fourth Stage Larvae.

1. Bases of inner anterior clypeal hairs nearly touching..................................2

Bases of inner anterior clypeal hairs widely separated..............................5

2. Inner anterior clypeal hairs branched distally..3

Inner anterior clypeal hairs simple..4

3. Inner anterior clypeal hairs with simple branching towards the end ; saddle hair simple..*nili* (p. 149)

Inner anterior clypeal hairs with compound branching towards the end ; saddle hair with 3–5 branches..*cinctus* (p. 148)

4. Outer anterior clypeal hairs with 40–50 branches ; inner shoulder hair very small, split into 2–4 branches ; apical antennal hair considerably longer than paired blades...*coustani* and *paludis* (p. 148)

Outer anterior clypeal hairs with 10–30 branches ; inner shoulder hair relatively well developed with 8–14 branches ; apical antennal hair not exceeding paired blades in length...*obscurus* (p. 147)

5. Outer anterior clypeal hairs tuft-like...6

Outer anterior clypeal hairs not tuft-like (simple, frayed or with a few short or long branches)...7

6. Spicules on short pecten teeth well developed, conspicuous...*pharoensis* (p. 159)

Spicules on short pecten teeth very poorly developed, inconspicuous........... *squamosus* (p. 160)

7. Saddle hair with 5 or more branches ; leaflets of abdominal palmate hairs on segments III–VII with short, spike-like tips.................*hancocki* (p. 184)

Saddle hair with fewer than 5 branches...8

8. Main abdominal tergal plates exceptionally wide and deep ; on segments V–VII their depth is more than half that of the segments ; median and paired accessory plates on III–VII included on main plates...........*funestus* (p. 150)

Main abdominal tergal plates narrower ; only one median accessory plate behind main plates on segments III–VII..9

9. Leaflets of abdominal palmate hairs without shoulders (tassel-like) ; plate of pecten strongly spiculate......................................*maculipalpis* (p. 158)

Leaflets of abdominal palmate hairs with at least some indication of shoulders...10

10. Leaflets of abdominal palmate hairs on III–VII with rounded tips and without linear terminations...*rufipes* (p. 157)

Leaflets of abdominal palmate hairs on III–VII with sharply pointed tips and usually with distinct linear terminations..11

11. Inner shoulder hair without chitinized base..12

Inner shoulder hair well developed and with chitinized base 13

12. Inner shoulder hair poorly developed, 5–8 branches ; thoracic palmate hair represented by 2–4 branched hair ; clypeal hairs delicate and frayed, outer hairs half or less than half length of inner..........................*gambiae* (p. 156)

Inner shoulder hair well developed, 13–20 branches ; thoracic palmate hair with 11–16 shoulderless leaflets ; clypeal hairs strong and coarsely frayed, outer hairs at least three-fourths length of inner.................*smithi* (p. 148)

13. Long mesopleural hairs both simple..14

Long mesopleural hairs with one feathered..17

14. Outer anterior clypeal hairs short, simple or bifid and bluntly pointed ; post-frontal hairs short, split into 2–4 branches...*moucheti* var. *nigeriensis* (p. 151)

Outer anterior clypeal hairs simple ; post-frontal hairs simple.................15

15. Saddle hair simple or bifid ; outer anterior clypeal hairs delicate, tapering... *hargreavesi* (p. 152)

Saddle hair with 4 branches..16

16. Posterior clypeal hairs long, reaching beyond bases of inner hairs ; outer anterior clypeal hairs delicate, tapering.......................*barberellus* (p. 153)

Posterior clypeal hairs short, not reaching bases of inner hairs ; outer anterior clypeal hairs bluntly pointed..................................*domicolus* (p. 153)

17. One of the long metapleural hairs feathered ; thoracic palmate hairs present...18

Both long metapleural hairs feathered ; thoracic palmate hair represented by a bifid or branched hair ; inner and outer clypeal hairs simple................. *pretoriensis* (p. 158)

18. Inner and outer clypeal hairs usually finely frayed ; thoracic palmate hairs with 7–11 shoulderless leaflets ; abdominal palmate hair on I rudimentary, 8–11 leaflets..*rhodesiensis* (p. 155)

Inner and outer clypeal hairs simple ; thoracic palmate hair with 14–19 leaflets ; abdominal palmate hair on I relatively large, about 14 leaflets................. *freetownensis* (p. 155)

Anopheles coustani, Laveran (fig. 21).

INNER CLYPEAL HAIRS.—Close together, bases sometimes in contact, simple.

OUTER CLYPEAL HAIRS.—Tuft-like, 40–60 branches.

POSTERIOR CLYPEAL HAIRS.—Very small, split into 2–3.

POST-FRONTAL HAIRS.—Strong, 8–11 branches.

APICAL ANTENNAL HAIR.—Considerably longer than blades, 4–13 branches.

SHAFT HAIR.—Conspicuous, 6–13 branches.

SHOULDER HAIRS.—Bases small, separate ; inner hair very small, split into 2–4, base unchitinized ; middle, longer, 8–12 branches.

LONG MESOPLEURAL HAIRS.—Both simple.

BASAL SPINES.—Small.

THORACIC PALMATE HAIRS.—10–15 narrow leaflets.

Abdominal Palmate Hairs.—I & II, rudimentary ; III–VII, well developed, tips may be sharp or blunt.

Tergal Plates.—Medium size and one free accessory plate.

Saddle Hair.—Simple.

Pecten.—Short teeth less than one-third length of ventral long tooth.

Breeding-places.—Ponds and swamps with plenty of vegetation, grass and upstanding weeds.

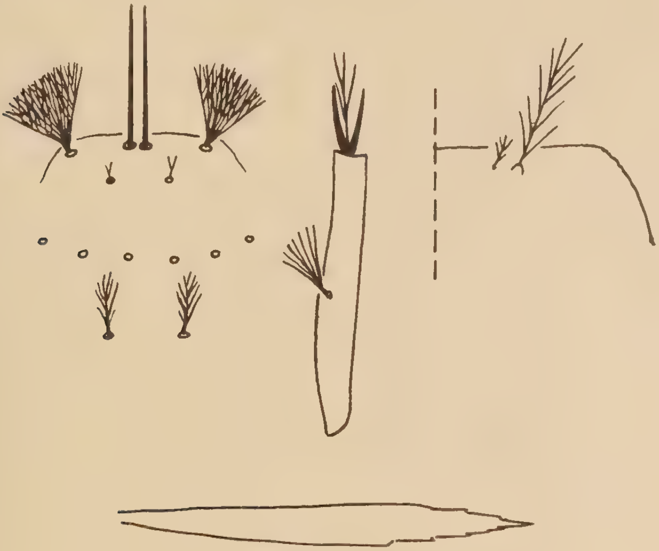

Fig. 21. *Anopheles coustani*, Laveran.

Anopheles obscurus, Grünberg.

Inner Anterior Clypeal Hairs.—Close together, simple.

Outer Anterior Clypeal Hairs.—Tuft-like, 10–30 branches.

Posterior Clypeal Hairs.—Short, simple, bifid or trifid.

Post-frontal Hairs.—Large, 8–10 branches.

Apical Antennal Hair.—Not longer than blades, branched 18–25.

Shaft Hair.—Conspicuous, branched 12–26.

Shoulder Hairs.—Bases well separated ; inner with no chitinized base, branched 8–14.

Long Mesopleural Hairs.—Both simple.

Thoracic Palmate Hairs.—9–15 leaflets.

Abdominal Palmate Hairs.—I & II, rudimentary ; III–VII, well developed, tips may be sharp or blunt.

Tergal Plates.—Medium size and one free accessory plate.

Saddle Hair.—Simple, short.

Pecten.—Short teeth one-third length of ventral long tooth.

Breeding-places.—Shaded ponds and swamps and sometimes at the edges of streams.

Anopheles cinctus, Newstead & Carter (fig. 22).

Inner Clypeal Hairs.—Near together, broad bases, long, compound, branching at outer half, 8–12 ultimate branches.

Outer Clypeal Hairs.—Close to and behind inner, short, stumpy, simple.

Posterior Clypeal Hairs.—Short, delicate, 2–5 branches.

Post-frontal Hairs.—Simple or bifid.

Apical Antennal Hair.—Extremely delicate, 7–14 branches.

Shaft Hair.—Minute, simple.

Shoulder Hairs.—Well developed, bases of inner and middle hairs separated ; inner with short flattened stem.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—Both simple.

Metapleural Hairs.—Both simple.

Thoracic Palmate Hairs.—Large, numerous unshouldered leaflets.

Abdominal Palmate Hairs.—I, small, developed ; II–VII, large, well developed.

Tergal Plates.—Broad, shallow ; median and paired accessory plates on II–VII.

Saddle Hair.—3–5 branches.

Pecten.—3 or 4 dorsal teeth longer than the rest, which are almost uniform.

Breeding-places.—Densely shaded, wooded hill streams.

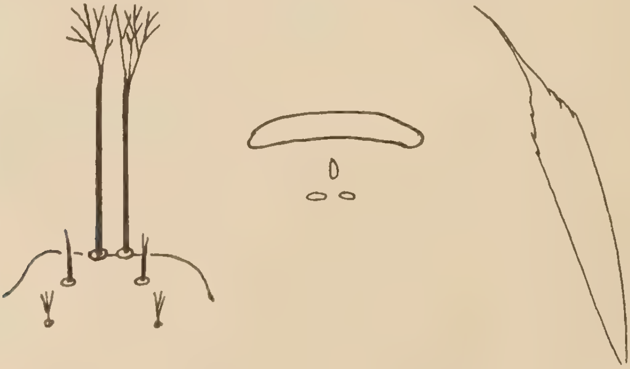

Fig. 22. *Anopheles cinctus,* Newstead & Carter.

Anopheles smithi, Theobald (fig. 23).

Inner Clypeal Hairs.—Apart, strong, simple or with some coarse fraying towards end.

Outer Clypeal Hairs.—Strong, three-fourths length of inner, frayed on basal half.

Posterior Clypeal Hairs.—Strong, long, reaching beyond bases of inner, frayed.

Post-Frontal Hairs.—Simple or bifid.

Apical Antennal Hair.—Stout, commonly simple.

Shaft Hair.—Long (length equal to width of antenna).

Shoulder Hairs.—Well developed ; bases well separated, inner with no chitinized tubercle.

Propleural Hairs.—Three simple.

Mesopleural Hairs.—Two simple.

Metapleural Hairs.—One simple, one split into two or three.

Thoracic Palmate Hairs.—11–16 leaflets.

Abdominal Palmate Hairs.—I, small but developed; II–VII, fully developed, shoulders serrated and fine filaments.

Tergal Plates.—Very small and one free accessory plate.

Saddle Hair.—Long, simple.

Pecten.—Teeth nearly all equal in length, long fine spicules.

Breeding-places.—Shaded, rocky bottom pools among tangled, dead or living vegetation.

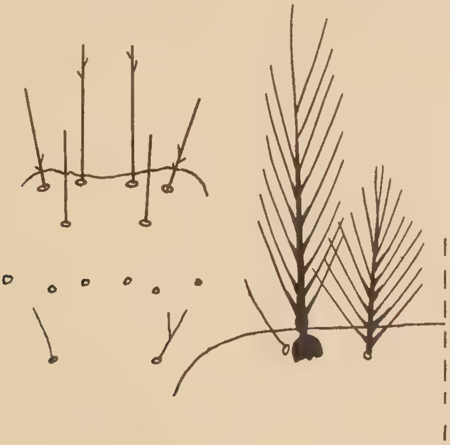

Fig. 23. *Anopheles smithi*, Theobald.

Anopheles nili, Theobald (fig. 24).

Inner Clypeal Hairs.—Near together, stout, tufted distally.

Outer Clypeal Hairs.—Near to inner, rather stout, simple.

Posterior Clypeal Hairs.—Far behind anterior, simple or split into two or three.

Post-frontal Hairs.—Short, simple.

Apical Antennal Hair.—2–4 branches.

Shaft Hair.—Inconspicuous.

Shoulder Hairs.—Well developed, large chitinized bases separated; inner with flattened stem.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—Two simple.

Metapleural Hairs.—Two simple.

Basal Spines.—Small.

Metathorax.—Small tergal plate common.

Thoracic Palmate Hairs.—Unusually well developed; 15–22 leaflets.

Abdominal Palmate Hairs.—I, small, well developed; II–VII, fully developed, filament arising from deep incision at shoulders.

TERGAL PLATES (fig. 24, A).—Wide and shallow and one free accessory plate.

SADDLE HAIR.—Simple, short.

PECTEN.—Difference in length between long and short teeth often very slight.

BREEDING-PLACES.—Among vegetation at the edges of clean rivers and streams.

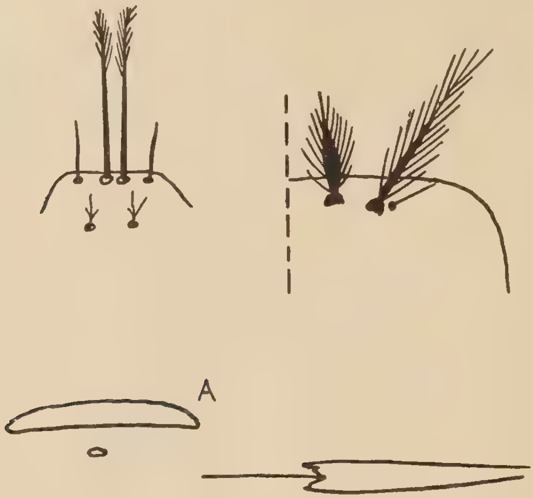

Fig. 24. *Anopheles nili*, Theobald.

Anopheles funestus, Giles (fig. 25).

FRONTO-CLYPEUS (fig. 25, A).—Dark transverse band.

INNER CLYPEAL HAIRS.—Well separated, simple.

OUTER CLYPEAL HAIRS.—Simple.

POSTERIOR CLYPEAL HAIRS.—Simple, reaching beyond bases of inner.

POST-FRONTAL HAIRS.—Simple or bifid.

APICAL ANTENNAL HAIR.—6–7 branches.

SHAFT HAIR.—Minute.

SHOULDER HAIRS.—Well developed ; bases with large chitinous tubercles often fused.

PROPLEURAL HAIRS.—Two simple, one feathered.

MESOPLEURAL HAIRS.—Two simple.

METAPLEURAL HAIRS.—One simple, one feathered.

BASAL SPINES.—Very short.

THORACIC PALMATE HAIR.—13–17 leaflets.

ABDOMINAL PALMATE HAIRS.—I, small, 11–15 leaflets ; II, developed ; III–VII, well developed, serrated shoulders and fine filaments always present.

TERGAL PLATES (fig. 25, B).—Very large ; IV–VII, covering large part of segments, posterior margin convex ; median and paired accessory plates included on main plate.

SADDLE HAIR.—Simple and long.

PECTEN.—Short teeth and some long ones spiculate ; irregular appearance.

Breeding-places.—Natural, permanent, clear waters containing vegetation, still or slowly moving and lightly shaded, e.g., weedy sides of streams, rivers, ponds and swamps.

Notes.—None of the following larvae has yet been recorded from W. Africa.

(*a*) *A. funestus* var. *confusus*, Evans & Leeson, differs from type form mainly in having tergal plates similar to those of *A. leesoni* (note (*e*)).

(*b*) *A. funestus* var. *fuscivenosus*, Leeson ; larva unknown.

(*c*) *A. rivulorum*, Leeson, differs from *A. funestus* chiefly in having branched post-frontal hairs resembling *leesoni* and in having main tergal plates very shallow and not including the median and paired accessory plates.

(*d*) *A. rivulorum* var. *garnhamellus*, Evans & Leeson, differs from type form in having paired accessory plates rarely present on more than 2 or 3 segments and often completely absent.

(*e*) *A. leesoni*, Evans, differs chiefly from *A. funestus* in having two longitudinal dark stripes on fronto-clypeus instead of a transverse band ; having branched post-frontal hairs and in having the paired accessory tergal plates not included in main tergal plates.

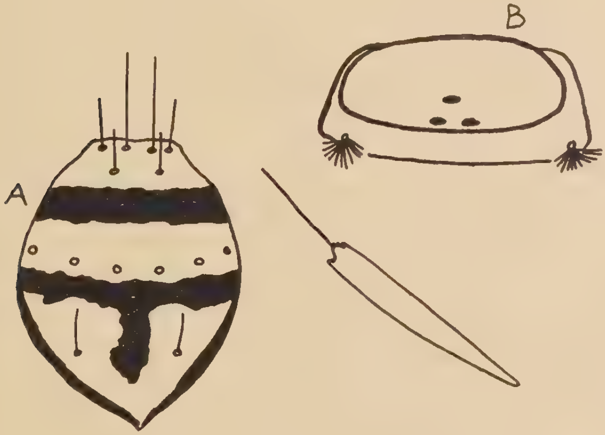

Fig. 25. *Anopheles funestus*, Giles.

Anopheles moucheti var. **nigeriensis,** Evans (fig. 26).

Inner Clypeal Hairs.—Apart, long, simple, finely tapered.

Outer Clypeal Hairs.—Simple or bifid and bluntly pointed.

Posterior Clypeal Hairs.—Short, simple or bifid.

Post-Frontal Hairs.—Short, split into 2–4.

Apical Antennal Hair.—2–4 branches.

Shaft Hair.—Small.

Shoulder Hairs.—Well developed ; lightly chitinized bases sometimes joined.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—Two simple.

Metapleural Hairs.—One simple, one feathered.

Basal Spines.—Rather short.

Thoracic Palmate Hair.—14–16 leaflets.

Abdominal Palmate Hairs.—I & II, developed; III–VII, fully developed, serrated shoulders, fine filaments.

Tergal Plates.—Moderate size; one free accessory plate.

Saddle Hair.—Long; split into 2 or 3 at tip.

Pecten.—Spicules numerous.

Breeding-places.—Among vegetation at sides of streams, rivers, pools.

Note.—Fig. 26, A, represents the kind of outer clypeal hair found on the type form *A. moucheti*, Evans.

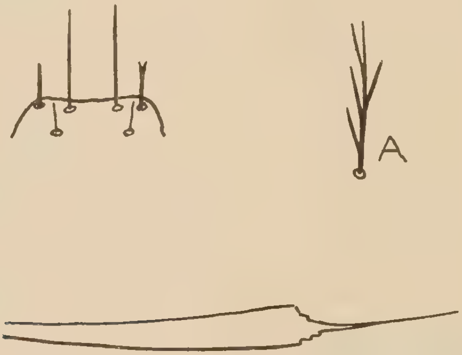

Fig. 26. *Anopheles moucheti* var. *nigeriensis*, Evans.

Anopheles hargreavesi, Evans.

Inner Clypeal Hairs.—Apart, long, simple.

Outer Clypeal Hairs.—Delicate, finely tapering, simple or bifid.

Posterior Clypeal Hairs.—Short, simple.

Post-Frontal Hairs.—Simple.

Apical Antennal Hair.—Four branches.

Shaft Hair.—Small.

Shoulder Hairs.—Well developed; lightly chitinized bases sometimes joined.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—Two simple.

Metapleural Hairs.—One simple, one feathered.

Basal Spines.—Rather short.

Thoracic Palmate Hairs.—14–16 leaflets.

Abdominal Palmate Hairs.—I, developed; II–VII, well developed, serrated shoulders, short fine filaments.

TERGAL PLATES.—Moderate size ; one free accessory plate.

SADDLE HAIR.—Long, simple, sometimes bifid.

PECTEN.—Spicules numerous.

BREEDING-PLACES.—Edges of streams among vegetation.

Anopheles domicolus, Edwards.

INNER CLYPEAL HAIRS.—Apart, simple.

OUTER CLYPEAL HAIRS.—Bluntly pointed, simple.

POSTERIOR CLYPEAL HAIRS.—One-third length of inner, not reaching bases of inner.

POST-FRONTAL HAIRS.—Simple.

APICAL ANTENNAL HAIR.

SHAFT HAIR.

SHOULDER HAIRS.—Well developed ; chitinized bases.

PROPLEURAL HAIRS.—Two simple, one feathered.

MESOPLEURAL HAIRS.—Two simple.

METAPLEURAL HAIRS.—One simple, one feathered.

THORACIC PALMATE HAIRS.—Present.

ABDOMINAL PALMATE HAIRS.—Sharply pointed tips.

TERGAL PLATES.—Moderate size ; one free accessory plate.

SADDLE HAIR.—Four branches.

BREEDING-PLACES.—No record.

Anopheles barberellus, Evans (fig. 27).

INNER CLYPEAL HAIRS.—Apart, long, simple, finely tapering.

OUTER CLYPEAL HAIRS.—More than half length of inner, simple, tapering.

POSTERIOR CLYPEAL HAIRS.—More than half length of inner, simple, tapering.

POST-FRONTAL HAIRS.—Simple.

APICAL ANTENNAL HAIR.—3–5 branches.

SHAFT HAIR.—Simple, small.

SHOULDER HAIRS.—Well developed ; chitinized bases fused.

PROPLEURAL HAIRS.—Two simple, one feathered.

MESOPLEURAL HAIRS.—Two simple.

METAPLEURAL HAIRS.—One simple, one feathered.

THORACIC PALMATE HAIRS.—Ten leaflets.

ABDOMINAL PALMATE HAIRS.—I & II, not fully developed ; III–VII, fully developed, small, serrated shoulders and tips spike-like ; no linear terminations.

TERGAL PLATES.—IV–VII, main plates rather broad, two-thirds distance between palmate hairs ; one free accessory plate.

SADDLE HAIR (fig. 27, A).—Four branches.

BREEDING-PLACES.—Springs, ditches, streams.

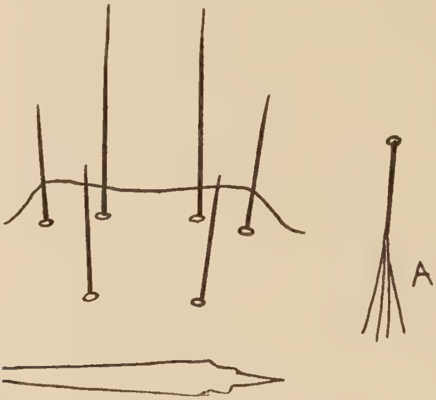

Fig. 27. *Anopheles barberellus*, Evans.

Anopheles hancocki, Edwards (fig. 28).

INNER CLYPEAL HAIRS.—Apart, simple, finely tapering.

OUTER CLYPEAL HAIRS.—Simple, stout, abruptly pointed.

POSTERIOR CLYPEAL HAIRS.—Simple, reaching to bases of inner.

POST-FRONTAL HAIRS.—Simple or bifid.

APICAL ANTENNAL HAIR.—Longer than blades, 3–7 branches.

SHAFT HAIR.—Minute.

SHOULDER HAIRS.—Well developed ; chitinized bases separate or joined.

PROPLEURAL HAIRS.—Two simple, one feathered.

MESOPLEURAL HAIRS.—Two simple (one occasionally bifid).

METAPLEURAL HAIRS.—One simple, one feathered.

BASAL SPINES.—Short.

THORACIC PALMATE HAIRS.—10–12 leaflets.

ABDOMINAL PALMATE HAIRS.—I, developed, 9–13 leaflets ; II–VII, well developed, leaflets broad, tips spike-like.

TERGAL PLATES.—Moderate size, one free accessory plate.

SADDLE HAIR (fig. 28, A).—Five or more branches.

PECTEN.—Short teeth abnormally short.

BREEDING-PLACES.—Margins of streams and pools.

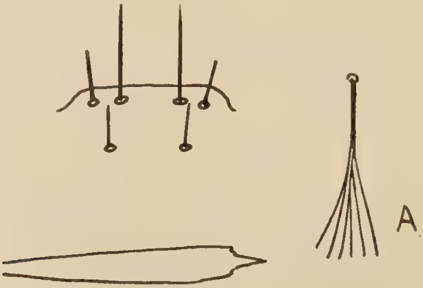

Fig. 28. *Anopheles hancocki*, Edwards.

Anopheles rhodesiensis, Theobald (fig. 29).

Inner Clypeal Hairs.—Apart, frayed.

Outer Clypeal Hairs.—Frayed.

Posterior Clypeal Hairs.—Simple.

Post-Frontal Hairs.—Simple.

Apical Antennal Hair.—2–5 branches.

Shaft Hair.—Nearly as long as width of shaft.

Shoulder Hairs.—Well developed; chitinized bases may be joined.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—One simple, one feathered.

Metapleural Hairs.—One simple, one feathered.

Basal Spines.—Small.

Thoracic Palmate Hairs.—Rudimentary, 9–11 leaflets.

Abdominal Palmate Hairs.—I, poorly developed, 8–11 leaflets; II, larger, 15–17 leaflets; III–VII, fully developed; serrated shoulders with or without linear terminations.

Tergal Plates.—Main, moderate size; one free accessory plate.

Saddle Hair.—Simple or bifid.

Breeding-places.—Margins of shady streams, pools.

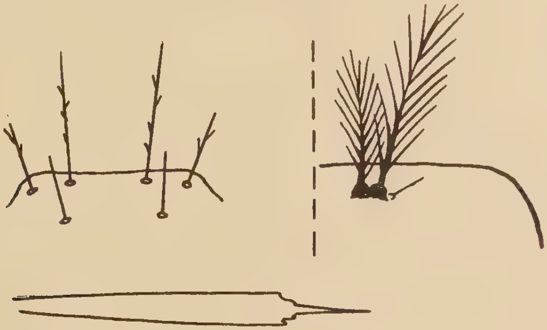

Fig. 29. *Anopheles rhodesiensis,* Theobald.

Anopheles freetownensis, Evans (fig. 30).

Inner Clypeal Hairs.—Long, simple.

Outer Clypeal Hairs.—Simple, half length of inner.

Posterior Clypeal Hairs.—Equal to outer, simple.

Post-Frontal Hairs.—Simple.

Apical Antennal Hair.—Short, two or three branches.

Shaft Hair.—Short.

Shoulder Hairs.—Well developed; large chitinized bases usually fused.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—One simple, one feathered.

Metapleural Hairs.—One simple, one feathered.

Basal Spines.—Small.

Thoracic Palmate Hairs (fig. 30, A).—14–19 leaflets.

Abdominal Palmate Hairs.—I–VII, well developed, leaflets with serrated shoulders and linear terminations.

Tergal Plates.—Small ; one free accessory plate.

Pecten.—Spicules well developed on all teeth.

Breeding-places.—Rock pools in stream-beds.

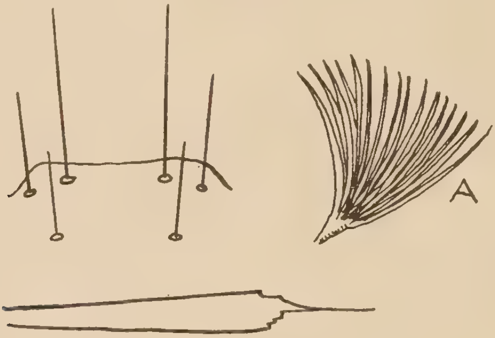

Fig. 30. *Anopheles freetownensis*, Evans.

Anopheles gambiae, Giles (fig. 31).

Inner Clypeal Hairs.—Apart, delicate, delicately frayed.

Outer Clypeal Hairs.—Simple or delicately frayed.

Posterior Clypeal Hairs.—Simple or delicately frayed ; short.

Post-Frontal Hairs.—Simple or bifid.

Apical Antennal Hairs.—3–6 branches.

Shaft Hair.—Short.

Shoulder Hairs.—Poorly developed, especially inner ; bases widely separated, inner without chitinous tubercle.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—Two simple.

Metapleural Hairs.—One simple, one feathered.

Basal Spines.—Long.

Thoracic Palmate Hairs.—Represented by 2–4 branched hair.

Abdominal Palmate Hairs.—I & II, poorly developed ; III–VII, well developed, serrations and fine filaments.

Tergal Plates.—Small ; one free accessory plate.

Saddle Hair.—Simple.

Pecten.—Short teeth spiculate.

Breeding-places.—Standing water exposed to sunlight nearly always devoid of living vegetation, *e.g.* puddles, borrow-pits, animal footprints, pools in river-beds and on their banks. Human activities often create breeding-places for this species—house building, railway and road construction, gold mining, etc.

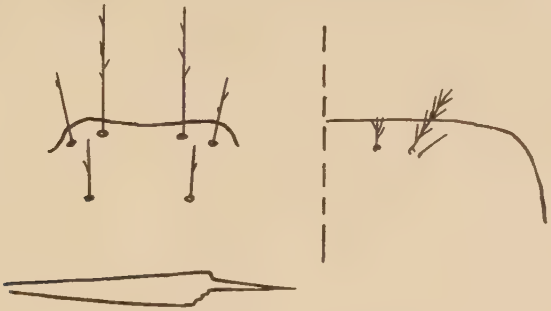

Fig. 31. *Anopheles gambiae*, Giles.

Anopheles rufipes, Gough (fig. 32).

Inner Clypeal Hairs.—Apart, branched.

Outer Clypeal Hairs.—Branched.

Posterior Clypeal Hairs.—Delicate, simple or bifid reaching beyond bases of inner.

Post-Frontal Hairs.—Simple or bifid.

Apical Antennal Hair.—Two or three branches.

Shaft Hair.—Minute.

Shoulder Hairs.—Well developed ; chitinized bases may be joined.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—One simple, one feathered.

Metapleural Hairs.—Two feathered.

Basal Spines.—Very short.

Metathorax.—Sometimes a pair of oval tergal plates.

Thoracic Palmate Hairs.—Represented by bifid hair (sometimes simple).

Abdominal Palmate Hairs.—I & II, rudimentary ; III-VII, well developed, tips rounded, no linear terminations.

Tergal Plates.—Moderate size, one free accessory plate.

Saddle Hair.—Simple or bifid.

Pecten.—First group of short teeth usually numerous, 6–8.

Breeding-places.—Large shallow fresh-water pools, pools in stream-beds, rock pools, marshes.

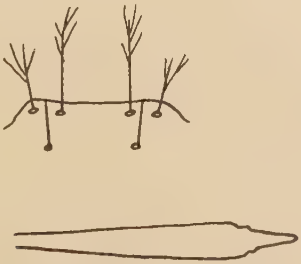

Fig. 32. *Anopheles rufipes*, Gough.

Anopheles pretoriensis, Theobald (fig. 33).

Inner Clypeal Hairs.—Apart, slender, simple.

Outer Clypeal Hairs.—Simple, half length of inner.

Posterior Clypeal Hairs.—Very delicate, simple, length equal to outer.

Post-Frontal Hairs.—Simple.

Apical Antennal Hair.—Three or four branches.

Shaft Hair.—Nearly as long as width of shaft, simple.

Shoulder Hairs.—Well developed ; chitinized bases small, may be joined.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—One simple, one feathered.

Metapleural Hairs.—Two feathered.

Basal Spines.—Small.

Thoracic Palmate Hairs (fig. 33, A).—Represented by hair, bifid, or with as many as 7 branches.

Metathorax.—Small paired tergal plates sometimes.

Abdominal Palmate Hairs.—I, very rudimentary ; II, poorly developed ; III–VII, well developed, small, serrated shoulders and linear terminations.

Tergal Plates.—Small ; one free accessory plate.

Saddle Hair.—Simple.

Pecten.—Teeth markedly spiculate.

Breeding-places.—Rock pools, streams and rivers, margins of swamps, often without shade or vegetation.

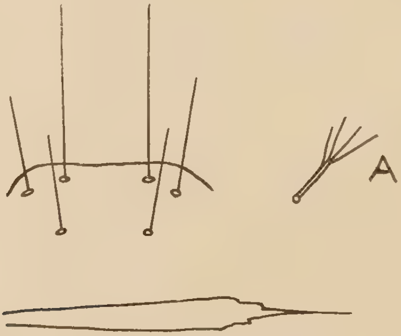

Fig. 33. *Anopheles pretoriensis*, Theobald.

Anopheles maculipalpis, Giles (fig. 34).

Inner Clypeal Hairs.—Apart, simple or frayed.

Outer Clypeal Hairs.—Simple or one branch.

Posterior Clypeal Hairs.—Simple, reaching well beyond bases of inner.

Post-Frontal Hairs.—Simple or bifid.

Apical Antennal Hair.—Long, split into two.

Shaft Hair.—Short.

Shoulder Hairs.—Large, well developed ; chitinized bases sometimes fused.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—One simple, one feathered.

Metapleural Hairs.—Two feathered.

Basal Spines.—Small.

Thoracic Palmate Hairs.—Represented by 2–4 branched hair.

Abdominal Palmate Hairs.—I & II, represented by 5–9 branched hairs; III, poorly developed; IV & V, tassel-shaped (fig. 34, A); VI & VII, as on V or rudimentary.

Tergal Plates.—Small, with one free accessory plate.

Saddle Hair.—Very long, simple.

Pecten.—Plate strongly spiculate.

Breeding-places.—Seepage water, cattle hoofprints, water sometimes little more than liquid mud, usually unshaded.

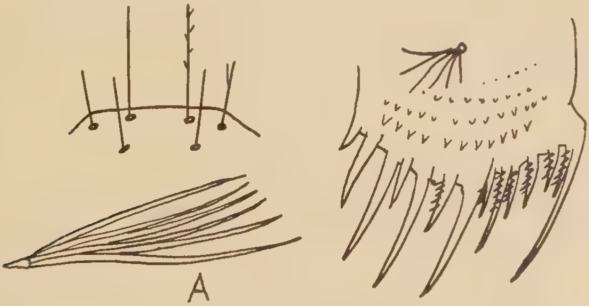

Fig. 34. *Anopheles maculipalpis*, Giles.

Anopheles pharoensis, Theobald (fig. 35).

Inner Clypeal Hairs.—Separate, long, branched, pinnate on distal half.

Outer Clypeal Hairs.—Tuft-like, 20–45 branches.

Posterior Clypeal Hairs.—2–5 branches.

Post-Frontal Hairs.—Simple or bifid.

Apical Antennal Hair.—2–4 branches.

Shaft Hair.—Minute.

Shoulder Hairs.—Well developed; bases chitinized and fused; inner flattened, 20–24 branches.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—Two simple.

Metapleural Hairs.—Two feathered.

Basal Spines.—Long.

Thoracic Palmate Hairs.—Small, 10–12 leaflets.

Abdominal Palmate Hairs.—I, fairly well developed, about 15 leaflets; II–VII, well developed, leaflets vary in width, linear termination sometimes absent.

Tergal Plates.—Moderate size; one free accessory plate.

Saddle Hair.—Simple.

Pecten.—Short teeth with well marked spicules.

Breeding-places.—In water containing much vegetation, *e.g.* swamps with grass, papyrus, *Pistia*, etc.

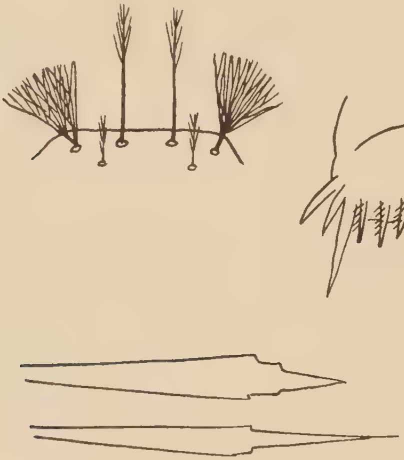

Fig. 35. *Anopheles pharoensis*, Theobald.

Anopheles squamosus, Theobald (fig. 36).

Inner Clypeal Hairs.—Separate, branched on distal half.

Outer Clypeal Hairs.—Commonly tuft-like, 8–28 branches.

Posterior Clypeal Hairs.—Simple, bifid or trifid.

Post-Frontal Hairs.—Simple or bifid.

Apical Antennal Hair.—2–4 branches.

Apical Antennal Blades.—Long, sometimes nearly half length of shaft.

Shaft Hair.—Minute.

Shoulder Hairs.—Well developed; bases chitinized and fused.

Propleural Hairs.—Two simple, one feathered.

Mesopleural Hairs.—Two simple.

Metapleural Hairs.—Two feathered.

Basal Spines.—Long.

Thoracic Palmate Hairs.—10–18 shoulderless leaflets.

Abdominal Palmate Hairs.—I, small, 12 leaflets; II–VII, well developed, linear terminations usually present.

Tergal Plates.—Moderate size ; one free accessory plate.

Saddle Hair.—Simple.

Pecten.—Spicules on short teeth inconspicuous or absent.

Breeding-places.—Ponds, borrow-pits, slow streams, hoof-marks, with vegetation.

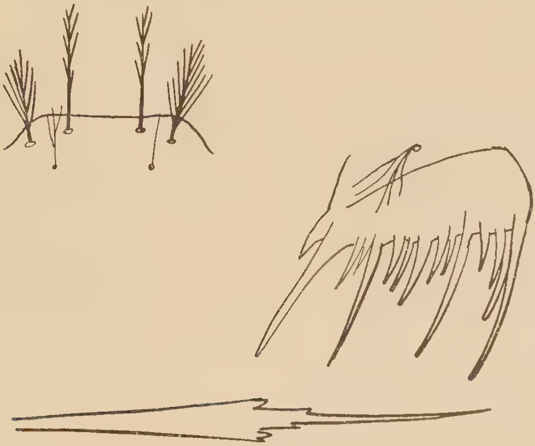

Fig. 36. *Anopheles squamosus*, Theobald.

CHALCID FLIES ATTACKING NOXIOUS BEETLES IN INDIA AND NEW GUINEA.

By Ch. Ferrière, D.Sc.

Imperial Institute of Entomology.

The Chalcidoidea mentioned in this paper are mostly parasites of the cotton stem-weevil, *Pempheres affinis*, Fst., in South India. They were bred by Mr. P. N. Krishna Ayyar during the years 1935 to 1938 and were sent in various collections to the Imperial Institute of Entomology for study. Another species, parasite of the Coconut Hispid, *Promecotheca papuana*, Csiki (*antiqua*, Ws.), has been added here, its description having been required for biological studies.

Among all the material sent from South India, seven species parasites of *Pempheres* have been found, which are :—

Dinarmus coimbatorensis, sp. nov.
Aplastomorpha calandrae, How.
Eupelmus urozonus, Dalm.
Eupelmella pedatoria, sp. nov.
Bruchocida orientalis, Crawf.
Euderus pempheriphila, Ayyar & Mani.
Entedon pempheridis, sp. nov.

The New Guinea parasite of *Promecotheca* has been named *Eurytoma promecothecae*, sp. nov.

Family Eurytomidae.

Eurytoma promecothecae, sp. nov.

♀♂. Body black. Antennae dark brown, scape yellowish at tip. Legs black, knees and end of tibiae yellow, tarsi white. Wings whitish, veins very light yellow.

♀. Head transverse, narrowed behind the eyes, strongly reticulate. Lateral ocelli closer to the front ocellus than to the eye margin. Eyes rounded. Cheeks as long as half the breadth of the eye, finely rugulose, with a strong carina going up behind the eye and a weaker one along the eye margin in front. Antennal furrow rather deep and short, strongly margined. Antennae inserted above the middle of the face, level with the middle of the eyes ; scape short, reaching scarcely beyond the front ocellus ; pedicel short, rounded ; 1st funicle joint elongate, a little more than 2·5 times as long as broad ; following joints gradually shorter, the 5th still 1·5 times as long as broad ; club narrow, as long as the two preceding joints together. Thorax strongly reticulate. Mesonotum a little shorter than the pronotum, the parapsidal furrows well defined ; scutellum elongate ; propodeum also strongly reticulate, excavated behind with rough and irregular transverse carinae along the middle line. Wings not quite reaching the tip of the abdomen ; submarginal vein about 4 times as long as the marginal vein, which is about as long as the postmarginal vein and the stigmal vein. Legs narrow ; hind coxae rugulose. Abdomen petiolate, the petiole scarcely as long as the hind coxae, with a thorn above near base and a rounded emargination below. Rest of abdomen smooth, oval, shorter than the thorax ; 5th segment the longest, 6th and 7th very short. Ovipositor very slightly protruding.

♂. Similar. Antennae elongate, scape short, slightly thickened, pedicel rounded, funicle joints elongate, terminating in a sort of petiole and each bearing two whirls of long hairs ; 1st joint about thrice longer than broad, the others somewhat shorter, the 5th not separated from the club by a petiole. Abdomen with the petiole longer than the hind coxae, the rest of the abdomen small and rounded, scarcely longer than the petiole.

Length : ♀ 2·2–3·2 mm. ; ♂ 1·5–2·3 mm.

New Britain : Gasmata, 1930, 1 ♀ 1 ♂ ; Rabaul, iii.1938, many ♀ and ♂, " Ex larvae of *Promecotheca antiqua* " (*J. L. Froggatt*).

This species may be recognised by its petiolate abdomen, the petiole being as long as or a little longer than the hind coxae, with a small thorn at base above and a rounded emargination below ; also the antennae are elongate with all funicle joints longer than broad ; and the marginal, stigmal and postmarginal veins are subequal in length.

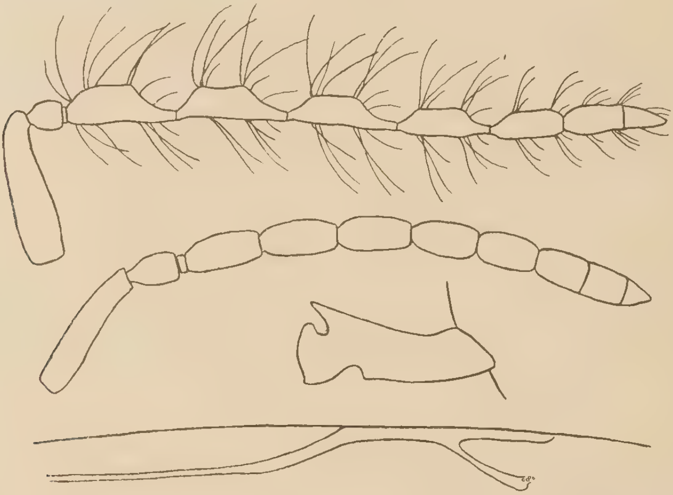

Fig. 1. *Eurytoma promecothecae*, sp. n. : antennae of male (above) and female, abdominal petiole and wing nervature.

Family Pteromalidae.

Dinarmus coimbatorensis, sp. nov.

♀♂. Head and thorax dark green ; abdomen aeneous, shining green at base. Antennae brown, scape, pedicel and annelli yellow. Tegulae yellow. Legs with coxae green, femora black with metallic reflections, especially on hind legs ; the trochanters, knees, ends of tibiae, and tarsi yellow ; the tibiae are almost entirely brown on the front legs, with a little more than the basal half brown on the middle legs, and with only a brown ring at base on the hind legs. The male has a large yellow spot at base of abdomen.

♀. Head transverse, narrow behind the eyes, entirely reticulate and only finely striate near the clypeus. Ocelli forming a low triangle, the lateral situated a little nearer to the front ocellus than to the eye margins. Mandibles each with 4 teeth. Antennae inserted above the middle of the face, the space between the front ocellus and the base of antennae shorter than the space between the antennae and the mouth. Scape narrow ; pedicel about twice as long as broad ; three transverse annelli ; 1st funicle joint elongate, broader and more than twice as long as the pedicel ; following joints gradually shorter, the 5th about 1·5 times as long as broad ; club short, oval, with three joints. Thorax broad, oval, finely reticulate ; pronotum margined in front ; mesonotum about twice as broad as long, the parapsidal furrows marked to a little over the middle ; scutellum broadly rounded at tip ; propodeum short, punctate, without median carina but with lateral folds ; spiracles oval. Wings broad, not reaching to the tip of the abdomen ; marginal vein thrice as long as the stigmal vein ; postmarginal vein almost twice as long as the stigmal vein. Legs strong, hind tibiae with two distinct spurs. Abdomen elongate and pointed at tip, narrower than the thorax, but longer than head and thorax together. A few specimens have the 6th and 7th abdominal segments less elongate and the abdomen is scarcely longer than head and thorax.

♂. Smaller ; antennae more elongate, with 2 annelli and 6 funicle joints ; all funicle joints about 1·5 times longer than broad, the last 2 slightly less. Abdomen depressed, oval, shorter than the thorax.

Length : ♀ 2·5–5 mm. ; ♂ 1·5–3 mm.

South India : Coimbatore, 1936–1938 (*R. N. Krishna Ayyar*) : 21 ♀ 9 ♂, ex *Pempheres affinis*, Fst., in *Triumfetta rhomboidea* ; 2 ♀ 1 ♂, ex *Pempheres* in cotton ; 2 ♀ 4 ♂, ex *Pempheres* in *Sida acuta* ; 1 ♀, ex *Pempheres* in *Sida spinosa* ; 1 ♀, ex *Pempheres* in *Corchorus olitorius* ; 8 ♀ 13 ♂, ex *Hypolixus truncatulus*, F., in *Amaranthus*.

This species may be distinguished from all other known species by the combination of the following characters : the medially incised clypeus, the punctate propodeum without median carina, the brown ring at base of hind tibiae, and the elongate abdomen. It is the first species known from India, but two other species have been described by Masi from Formosa.

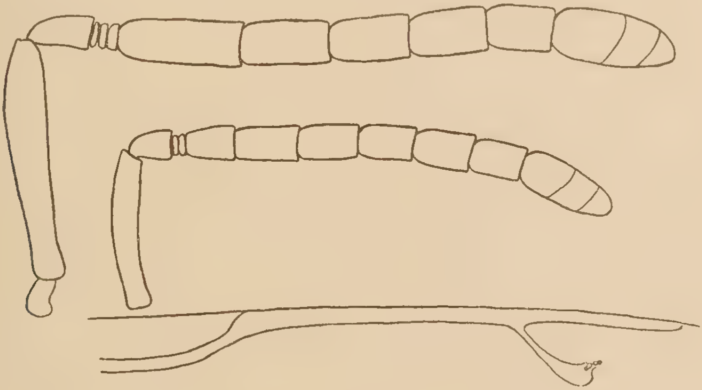

Fig. 2. *Dinarmus coimbatorensis*, sp. n. : antennae of female (above) and male ; wing nervature.

Aplastomorpha calandrae, Howard.

This is a cosmopolitan species, found mainly as a parasite of beetles in stored products : *Calandra*, *Sitodrepa*, *Lasioderma*, *Pachymerus*, *Bruchus*. It is curious to find it attacking also stem-boring weevils. We have examined 9 ♀ and 19 ♂ sent as parasites of *Pempheres* in cotton, and we are unable to find any difference from the large number of specimens from different parts of the world in the British Museum. The *Pempheres* parasites are on the average larger than the *Calandra* parasites, but there are also smaller specimens among them, and the males and females are similar in structure and coloration.

This is probably the same species as the parasite of *Pempheres* described by Ramakrishna Ayyar and Mani under the name of *Neocatolaccus indicus*. Their description of the female agrees almost exactly. *Neocatolaccus*, Ashm., and *Aplastomorpha*, Crawf., are very closely related genera ; both have 3 annelli in the antennae and a short propodeum with a median carina. They may have to be reunited, but for the present can be distinguished by the following characters :

Neocatolaccus, Ashm. Marginal vein distinctly longer than the postmarginal vein. Abdomen elongate, longer than head and thorax together. Thorax with appressed white pubescence.

Aplastomorpha, Crawf. Marginal vein about as long as the postmarginal vein. Abdomen not much longer than the thorax. Pubescence on head and thorax less distinct.

Family Eupelmidae.

Eupelmus urozonus, Dalm.

It is with some doubt that we identify the Indian specimens with this common Palaearctic species. But we cannot find good morphological differences to distinguish them, and *E. urozonus*, which has been found as far as Egypt and Asiatic Turkey, may have a wider distribution than is generally known. Few specimens have been received, labelled : ex *Pempheres affinis* on cotton (3 ♀ 1 ♂), ex *Pempheres affinis* in *Sida acuta* (1 ♀) and ex *Hypolixus truncatulus* in *Amaranthus* (2 ♀ 1 ♂). They may be distinguished from other Indian species like *tachardiae*, How., and *javae*, Gir., by their dark green scape.

Eupelmella pedatoria, sp. nov.

♀. Black, with greenish and partly purplish reflections on head, thorax and base of abdomen ; face shining purple, middle of mesonotum more or less violaceous. Antennae black, the pedicel and first funicle joints with greenish reflection, scape yellow. Legs black, only the base of tibiae, the spur and tarsi of middle legs yellow. Ovipositor yellow with base, tip and underside black.

Head smooth, very finely transversely striate, narrowed behind the eyes. Ocelli very small, the lateral closer to the eyes than to the front ocellus. Eyes oval ; cheeks as long as half the length of an eye. Face shagreened. Antennae inserted slightly above the lowest level of the eyes ; scape narrow, reaching scarcely the front ocellus ; pedicel narrow, about three times as long as broad ; annellus transverse ; 1st funicle joint a little longer than the pedicel, the following joints gradually shorter and broader, the 7th subquadrate ; club almost as long as the three last funicle joints together. Thorax almost smooth, very finely shagreened on pronotum and mesonotum and striate on mesopleurae ; scutellum closely sculptured, dull. Pronotum elongate, narrowed in front, with a transverse carina bearing very long ciliae arranged in two thin vertical brushes. Mesonotum concave, with a faint furrow along the posterior half ; parapsides longitudinally carinate, with a row of white ciliae. Scutellum longer than broad ; axillae also elongate, meeting in the middle. Postscutellum very large, smooth, with the lateral and posterior margins straight. Propôdeum very short, annular, with the spiracles on two small prominences. Wings rudimentary, oval, reaching little beyond the tip of the scutellum. Legs narrow and rather long, the front tarsi longer than the tibiae, the hind coxae with a pointed thorn above. Abdomen oval, not depressed, about as broad and as long as the thorax ; the 1st tergite strongly emarginate at middle of hind margin ; 2nd and 3rd tergites with the hind margins less emarginate. Ovipositor about as long as one-fifth of the abdomen.

Length : 1·4–3·5 mm. Some specimens bred from eggs are only 1 to 1·2 mm. long.

South India : Coimbatore, 1937–1938, 7 ♀, ex *Pempheres affinis*, Fst., on cotton (1 ♀ said to have been reared on pupa of *Euderus*) ; 3 ♀, ex *Hypolixus truncatulus*, F., in *Amaranthus* ; 4 ♀, ex eggs of *Hypolixus* (*R. N. Krishna Ayyar*).

This is the first known Oriental species of the genus *Eupelmella*, Masi. But species described in *Eupelmus*, Dalm., may be found to belong here. The differences between these two genera have not been fully recognised, even since Masi described *Eupelmella* in 1919. The main character by which *Eupelmella* can be distinguished from *Eupelmus* is the large development of the postscutellum, which is more or less flat and with straight side and hind margins, the front margin being curved around the tip of the scutellum. This postscutellum is always much larger than the very short propodeum. The mesonotum is regularly curved in the middle, without very distinct parapsidal furrows and with lateral carinae, and the pronotum is distinctly separated from the mesonotum.

This Indian species is specially related to the European *E. müllneri*, Ruschka, and the North African *E. schizomyiae*, Masi.

Bruchocida orientalis, Crawford.

Only one female of this species, with the head broken, has been received from Coimbatore, labelled : " 7.vii.37, on *Pempheres* in *Triumfetta rhomboidea*." It agrees exactly with Crawford's description made from specimens from India, Bangalore, parasites of *Bruchus chinensis*.

Family Eulophidae.

Euderus pempheriphila, Ayyar and Mani.

This species has been well described and seems to be a common parasite of *Pempheres affinis*. We have the following series from Coimbatore : 33 ♀ 22 ♂, ex *Pempheres* on cotton ; 1 ♀, ex *Pempheres* in *Sida acuta* ; 1 ♀, ex *Hypolixus truncatulus* in *Amaranthus*.

Entedon pempheridis, sp. nov.

♀♂. Head and thorax of female black, with faint greenish reflections ; abdomen with the basal half shining bluish-green, the posterior half aeneous black. The male is bluish green, the abdomen aeneous green with a large yellow spot at base. Antennae black, more or less greenish, especially on pedicel ; scape yellow. Legs black, with dark green reflections ; knees, end of front tibiae, terminal half of middle tibiae and the hind tibiae, except a broad ring near base, yellow. In the male the tibiae are entirely yellow, except a longitudinal line on the front tibiae.

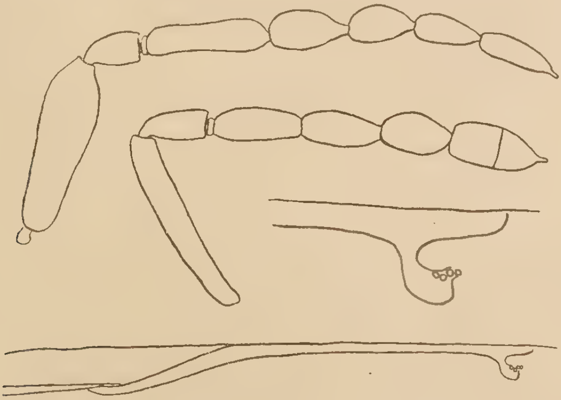

Fig. 3. *Entedon pempheridis*, sp. n. : antennae of male (above) and female ; wing nervature and stigmal vein more enlarged.

♀. Head transverse, truncate just behind the eyes; occiput slightly excavate and separated from the vertex by a carina. Vertex and face reticulate, more finely near the clypeus. Eyes large, oval; cheeks short and smooth. Ocelli forming a low triangle, the lateral placed near the occipital carina and much closer to the eye margin than to the front ocellus. Mandibles with two teeth. Antennae inserted below the middle of the face, slightly above the lower level of the eyes; scape narrow, reaching not quite to the front ocellus; pedicel 2·5 times as long as broad; one very small annellus; 1st funicle joint elongate, longer than the pedicel; 2nd a little shorter than the 1st; 3rd oval, broader, as long as the pedicel; club with two joints, not much longer than the 1st funicle joint. Pronotum short, transverse. Mesonotum and scutellum strongly reticulate, dull; parapsidal furrows, complete but not deep; scutellum a little longer than the mesonotum. Propodeum large, smooth, with a median carina bordered by two furrows which converge behind; lateral furrows well marked; spiracles small, rounded. Wings large, reaching to or a little beyond the tip of the abdomen; marginal vein elongate, narrower at end than at base; stigmal vein very short, almost sessile; postmarginal vein a little longer than the stigmal vein. Legs strong, hind femora somewhat thickened. Abdomen oval, about as long as the thorax; petiole short, broader than long. Ovipositor not protruding.

♂. Antennae narrower and longer, scape slightly thickened, pedicel about 1·5 times as long as broad; 1st funicle joint narrow and long, 2·5 times as long as the pedicel, narrower in the middle; the three following joints oval, shorter than the 1st; club not divided, a little longer than the 4th funicle joint and pointed. Abdomen short oval, the petiole about twice as long as broad, shorter than the hind coxae.

Length: ♀ 1·5–3·4 mm.; ♂ 1·5–2·2 mm.

South India, Coimbatore, 1937–1938 (*P. N. Krishna Ayyar*): 77 ♀ 30 ♂, ex *Pempheres affinis* in *Triumfetta rhomboidea*; 1 ♀, ex *Pempheres* on cotton; 1 ♀, ex *Pempheres* in *Sida acuta*; 4 ♀ 3 ♂, ex *Pempheres* in *Corchorus olitorius*; 8 ♀ 4 ♂, ex *Apion* grubs in *Corchorus*; 3 ♀ 2 ♂, ex *Lobotrachelus* in *Hibiscus vitifolius*; 1 ♂, ex *Hypolixus truncatulus* in *Amaranthus*.

This species belongs to the same group as several other species parasitising weevils in Europe, Africa and America, like *E. cioni*, Thoms., *E. pharnus*, Walk., *E. perturbatus*, Walk., *E. tachypterelli*, Gah., and others. It may be distinguished specially by the yellow scape, the relative size of the antennal joints and the coloration of the legs, with a black ring at the base of the hind tibiae in the female. Most species of this group have the scape dark coloured and the yellow scape in this species may suggest the related genus *Derostenus*, Westw. But *Derostenus* has a finer sculpture on head and thorax and the occiput is not so sharply margined just behind the eyes.

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st October and 31st December, 1938 :—

Agricultural Officer, Quetta :—12 Diptera, 23 Parasitic Hymenoptera, and 8 Rhynchota ; from Baluchistan.

Agricultural Research Institute, Wad Medani :—218 Coleoptera and 5 Mites ; from the Sudan.

Mr. P. N. Krishna Ayyar :—55 Coleoptera and 25 Parasitic Hymenoptera ; from South India.

Mr. E. Ballard, Chief Plant Protection Officer :—2 Diptera and 5 Coccinellidae ; from Palestine.

Dr. F. S. Bodenheimer :—24 Diptera, 23 Coleoptera, 10 Parasitic Hymenoptera, 12 other Hymenoptera, 23 Lepidoptera, and 30 Rhynchota ; from Palestine.

Mr. E. McC. Callan :—13 Coleoptera ; from the British West Indies.

Chief Entomologist, Pretoria :—4 Diptera, 91 Coleoptera, 43 Parasitic Hymenoptera, 12 Formicidae, 1 species of Coccidae, 6 other Rhynchota, 8 Orthoptera, and 2,000 Mites ; from South Africa.

Father P. A. Conrads :—25 Orthoptera ; from Tanganyika Territory.

Mr. G. H. Corbett, Government Entomologist :—18 Diptera, 40 Coleoptera, 29 Parasitic Hymenoptera, 6 Formicidae, 18 Lepidoptera, 47 Isoptera, and 14 Rhynchota ; from Malaya.

Coryndon Memorial Museum :—11 Tabanidae, 6 *Glossina*, 577 other Diptera, 131 Hymenoptera, and 103 Lepidoptera ; from East Africa.

Mr. A. C. Cotton :—15 Formicidae ; from South India.

Mr. A. Cuthbertson, Entomologist :—109 Diptera, 4 Coleoptera, 26 Parasitic Hymenoptera, 500 Isoptera, 31 Rhynchota, and 2 Orthoptera ; from Southern Rhodesia.

Dr. A. da Costa Lima :—45 Coleoptera ; from Brazil.

Dr. J. Davidson :—27 Coleoptera ; from South Australia.

Mr. L. P. de Bussy :—30 Parasitic Hymenoptera ; from Holland.

Director of Agriculture, Mauritius :—25 Parasitic Hymenoptera, 1 species of Coccidae, and 1 species of Mite.

Director of Agriculture, North Borneo :—4 *Tabanus*, 10 other Diptera, 2 Coleoptera, 30 Parasitic Hymenoptera, 2 Lepidoptera, and 4 Rhynchota.

Director of Medical Services, Dar-es-Salaam :—12 Simuliidae ; from Tanganyika Territory.

Mr. L. J. Dumbleton, Cawthron Institute :—7 Parasitic Hymenoptera ; from New Zealand.

Mr. G. S. Dun :—3 Coleoptera and 8 Chrysopidae ; from the Fiji Islands.

Entomologist, Mandalay :—6 Rhynchota ; from Burma.

Mr. J. L. Froggatt, Government Entomologist :—4 Diptera, 63 Coleoptera, 18 Parasitic Hymenoptera, 3 other Hymenoptera, 17 Lepidoptera, 19 Rhynchota, 4 Planipennia, and 15 Ticks ; from New Guinea.

Mr. J. C. M. GARDNER, Systematic Entomologist :—57 Diptera and 31 pupa cases, 553 Parasitic Hymenoptera and 100 cocoons ; from the United Provinces, India.

Mr. S. GARTHSIDE :—52 Parasitic Hymenoptera and 52 cocoons ; from England.

Mr. S. S. GONZALES :—12 Coleoptera and 12 early stages ; from the Philippine Islands.

GOVERNMENT ENTOMOLOGIST, COIMBATORE :—6 Diptera, 4 Coleoptera, and 27 Lepidoptera ; from South India.

GOVERNMENT ENTOMOLOGIST, LYALLPUR :—207 Diptera and 98 species of Coccidae ; from the Punjab, India.

GOVERNMENT ENTOMOLOGIST, NJALA :—29 *Stomoxys* ; from Sierra Leone.

THE GOVERNOR, ASMARA :—48 Orthoptera ; from Eritrea.

Mr. G. H. HAMMOND, Entomologist :—400 Coleopterous early stages ; from Canada.

Mr. H. HARGREAVES, Government Entomologist :—506 Diptera, 12 Coleoptera, 216 Lepidoptera and 25 early stages, 382 Rhynchota, and 6 Orthoptera ; from Uganda.

Mr. W. V. HARRIS, Entomologist :—3 Spiders ; from Tanganyika Territory.

Mr. G. V. HUDSON :—58 Coleoptera ; from New Zealand.

INDIAN LAC RESEARCH INSTITUTE, NAMKUM :—28 Diptera and 21 pupa-cases 89 Parasitic Hymenoptera and 54 cocoons ; from India.

INSTITUT DES PARCS NATIONAUX DU CONGO BELGE, BRUXELLES :—76 Coleoptera ; from the Belgian Congo.

INSTITUTE FOR PLANT DISEASES, BUITENZORG :—42 Parasitic Hymenoptera ; from the Dutch East Indies.

Mr. R. B. JACKSON :—29 Diptera ; from Hong Kong.

Mr. B. KASSANIS :—7 Coleoptera ; from Greece.

Mr. T. W. KIRKPATRICK, Entomologist :—2 Diptera, 80 Lepidoptera and 40 early stages ; from Tanganyika Territory.

Miss J. LAING :—198 Parasitic Hymenoptera and 5 cocoons ; from Queensland.

Dr. H. S. LEESON, London School of Tropical Medicine :—15 Coleoptera, 18 Rhynchota, 10 Mites, and 20 Crustacea ; from Greece.

Mr. R. A. LEVER, Government Entomologist :—12 Culicidae, 4 Nycteribiidae, 250 other Diptera and 32 pupa-cases, 68 Coleoptera and 60 early stages, 85 Parasitic Hymenoptera, 202 other Hymenoptera, 35 Lepidoptera, 6 species of Coccidae, 2 species of Aphidae, 1 species of Aleurodidae, 85 other Rhynchota, 4 Orthoptera, 9 Planipennia, 100 Mites, 10 Crustacea, and 6 Worms ; from the Fiji Islands.

MEDICAL ENTOMOLOGIST, KHARTOUM :—127 Culicidae ; from the Sudan.

Prof. F. J. MEGGITT :—30 Parasitic Hymenoptera and 10 larvae, and 1 species of Worm ; from Burma.

Mr. H. M. MORRIS, Government Entomologist :—28 Parasitic Hymenoptera and 54 Lepidoptera ; from Cyprus.

Mr. R. W. MUNGOMERY :—10 Diptera, 5 Parasitic Hymenoptera, and 1 species of Coccidae ; from Queensland.

MUSÉE DU CONGO BELGE, TERVUEREN :—12 Parasitic Hymenoptera and 6 Formicidae ; from the Belgian Congo.

Narborough (F.M.S.) Rubber Estates, Ltd.—3 Coleoptera and 11 early stages; from Malaya.

Mr. F. B. Notley, Entomologist :—200 Lepidoptera and 100 early stages; from Tanganyika Territory.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—2 Coleopterous larvae, 250 Formicidae and early stages, 10 Lepidoptera, 50 Isoptera, and 2 Blattidae; from British Somaliland.

Dr. M. Pfaundler :—52 Coleoptera; from South Persia.

Mr. J. de B. R. Queiroz :—13 Diptera, 12 Coleoptera, 9 Parasitic Hymenoptera, and 20 Rhynchota; from Angola.

Mr. P. Regnier :—17 Diptera and 30 Parasitic Hymenoptera; from Morocco.

Royal Botanic Gardens, Kew :—6 Coleoptera; from England: and 24 Coleoptera; from Mexico.

Dr. H. Sachtleben :—140 Parasitic Hymenoptera and 22 cocoons; from Germany.

Mr. B. Schaerffenberg :—11 Dipterous larvae, 290 Coleopterous larvae, and 16 Lepidopterous larvae; from Germany.

Selangor Museum :—184 Coleoptera; from Malaya.

Nihat Shevket Iyriboz :—2 species of Mites; from Turkey.

Mr. E. R. Speyer :—3 Lepidopterous larvae; from England.

Mr. C. F. M. Swynnerton :—364 Tabanidae, 178 other Diptera, 568 Coleoptera, 128 Hymenoptera, 24 Lepidoptera, 2 Isoptera, 154 Rhynchota, 173 Orthoptera, 3 Dermaptera, 10 Planipennia, 2 Odonota, 4 Ticks, 11 Mites, 46 Spiders, 67 Crustacea, and 4 Snail Shells; from Southern Rhodesia.

Dr. A. L. Tonnoir, Senior Research Officer :—1 Curculionid; from Australia.

Mr. C. E. Tottenham :—50 slides of Coleopterous larvae; from England.

Prof. J. van den Brande :—7 Parasitic Hymenoptera and 2 Lepidoptera; from Belgium.

Mr. P. Vayssière :—21 Parasitic Hymenoptera; from France.

Mr. D. Vesey-Fitzgerald :—59 Coleoptera, 60 Parasitic Hymenoptera, 50 Lepidoptera, and 17 tubes of Coccidae; from the Seychelles.

Mr. F. Wilson :—2 Diptera, 15 Parasitic Hymenoptera, and 10 cocoons; from France.

Mr. J. W. Wilson :—4 Coleopterous larvae; from Florida.

Mr. E. C. Zimmerman :—29 Coleoptera; from the Solomon Islands.

THE HOLLY LEAF-MINER (*PHYTOMYZA ILICIS*, CURT.) AND ITS PARASITES.*

By Ewen Cameron, Ph.D., B.Sc., F.R.E.S.
Farnham House Laboratory, Imperial Institute of Entomology.

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Introduction.

On the West Coast of British Columbia, where the mild humid climate is particularly favourable to its growth, European Holly (*Ilex aquifolium*, L.) is rather extensively cultivated. Because it cannot be grown successfully in other parts of North America, an important industry has sprung up on the Pacific North-West Coast (British Columbia in Canada and W. Washington and N.W. Oregon in the United States), and the sales of cut holly from this region amount to several hundred thousand dollars annually. For planting as an ornamental tree in public parks and private estates it is also in good demand, and many fine specimens have been grown, especially in the city of Vancouver. The only " fly in the ointment," so far as the nurserymen are concerned, is literally a fly—*Phytomyza ilicis*, Curt., or the Holly Leaf-miner, an insect whose larvae burrow in the mesophyll and produce large unsightly blotches or mines on the surface of the leaves. As many as 75 to 80 per cent. of the latter may be disfigured annually in this way, and as a consequence, the cut foliage, from a commercial point of view, is considerably reduced in value. The trees themselves are also rendered less ornamental and attractive, and although the effect is not very apparent, it is quite possible that they suffer somewhat in health by the wholesale removal of such a large mass of chemically active cells.

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* Part of thesis approved for the Degree of Doctor of Philosophy in the University of Edinburgh.

Like its host, the Holly Leaf-miner is a native of north-west Europe, and the phenomenal success which it has attained in British Columbia is said to be due to the absence of its natural enemies from this area. Since these latter apparently failed to accompany the fly when its was accidentally introduced into Canada, the Dominion authorities, strengthened by the knowledge that chemical control had been unsuccessful, decided to make good this deficiency in the fauna and asked the Imperial Institute of Entomology to secure the necessary parasites. In compliance with this request, and as a preliminary to the work of collection and export, the present writer made a comprehensive study of the various species of Hymenoptera which attack the immature stages of the leaf-miner in England, and the results of this investigation, preceded by a general account of the biology of the fly itself, are set down in the following pages.

An account of the biological control of *P. ilicis* will be published in a separate paper at a later date.

Systematics and Biology of Phytomyza ilicis.

Systematic Position and Synonymy.

Phytomyza ilicis belongs to the Family Agromyzidae (Diptera), a family of small flies, the larvae of which are usually leaf-miners. According to Imms (1934) these larvae are characterized by sphaeroidal concretions of calcium carbonate in the malpighian tubes. Similar deposits have been observed in the larvae of the Holly Leaf-miner, but in this species they occur not in the malpighian tubes but in nucleated cells between the coils of the fat-body.

On reading through the literature dealing with *Phytomyza* it was discovered that the synonymy and exact identity of the Dipterous flies whose larvae mine the leaves of holly was in a state of some confusion. Reference was made to the published works of Curtis (1846), Goureau (1851), Frost (1923), Hering (1927), Hendel (1918), and Loew (1863 and 1872), and the conclusion was reached that although many different names have been applied to these flies, in reality there are only two recognisable species—(1) *Phytomyza ilicis*, Curt., and (2) *P. ilicicola*, Loew. In his monograph on the leaf-mining Diptera of North America, Frost (1923) also reduced the number to two—(1) *Phytomyza aquifolii*, Goureau, which he believed to be conspecific with *P. ilicis*, Kalt., and (2) *P. ilicis*, Curt., synonymous with *Chromatomyia ilicis*, Curt., *Phytomyza obscurella*, Weyenb., *P. ilicicola*, Loew, and *P. obscurella* var. *ilicicola*, Melander ; but there is sufficient evidence to show that this author's nomenclature is incorrect. So far as *aquifolii*, Goureau, is concerned, it is quite clear from the latter's description of this fly—which, incidentally is extremely short and inadequate—that he was dealing with *ilicis*, Curt. The mine of *aquifolii*, which he figures, is exactly similar to that of *ilicis*. In addition, both Hering (1927) and Hendel (1918) agree that Goureau in 1851 was dealing with the same species which Curtis had described five years previously, so that it is perfectly evident that *aquifolii* is a synonym, and *ilicis*, Curt., having the prior claim, must be regarded as the valid name for this species. Since the latter, so far as I am aware, is the only species of *Phytomyza* that attacks *I. aquifolium* in the Palearctic region, it must be regarded as the insect which is the subject of the present investigation. It is obvious, however, from his descriptions that Frost actually observed two different kinds of flies, and since we have shown that one of these is *ilicis*, Curt. (European origin), the other, which *he* calls *P. ilicis*, Curt., with its numerous synonyms, can only be *ilicicola*, Loew, which was described from North America in 1863. This latter is distinct from *ilicis*, and the difference between the two is most clearly brought out in fig. 1, where the mines of both are portrayed—that of *ilicis* being broad and blotchy, while that of *ilicicola* is linear and serpentine. When he discovered this Nearctic form, Loew called it *P. ilicis*, Loew, but nine years later (1872) he realised that this name had already been appropriated by Curtis for the European species, so he altered it to *ilicicola*. The correct identity and synonymy of these flies is therefore as follows :—

1. *Phytomyza ilicis*, Curtis ; synonyms, *Chromatomyia ilicis*, Curt., and *P. aquifolii*, Goureau.
2. *Phytomyza ilicicola*, Loew ; synonyms, Frost's *P. ilicis*, Curt., *P. obscurella*, Weyenb., and *P. obscurella* var. *ilicicola*, Melander.

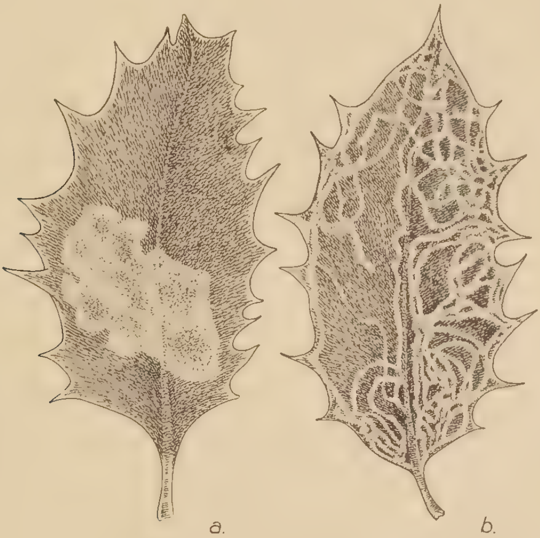

Fig. 1. Holly leaves mined by (*a*) *Phytomyza ilicis*, Curt. ; (*b*) *P. ilicicola*. (b. redrawn from Essig.) (× $\frac{3}{4}$).

The main points of difference between *Phytomyza ilicis* and *ilicicola* appear to be as follows :—

ilicicola	*ilicis*
First two antennal segments brown, third black.	Antennae entirely black.
Arista at most 2·25 times as long as third antennal joint.	Arista 3 times as long as third antennal joint.
Thorax and femora more strongly dusted with grey.	Thorax and femora darker.
Last segment of abdomen in female with yellow incisure.	Yellow incisure absent.

According to Frost there are 5–9 slits in the posterior stigmata of the larva of *ilicis*, and twenty in that of *ilicicola*.

Distribution and Host-plants.

P. ilicis is fairly common in Europe, especially in England, France, Germany and Holland, and as a result of accidental introduction it is now present in the New World, in both Canada and the United States. *P. ilicicola*, on the other hand, is said to be indigenous to North America and has not been recorded outside that country. This latter species, according to Essig (1929), attacks both European holly (*Ilex aquifolium*) and American holly (*I. opaca*), while *ilicis* appears to be confined to the European species, with its numerous varieties.

Life-history.

Two separate accounts of the life-history of the Holly Leaf-miner have already been published, one in England, by Miall and Taylor (1907), dealing chiefly with the anatomical structure of the fly and its various developmental stages, and the other in Canada by Downes (1931), who was more concerned with chemical measures of control.

The imago emerges from the puparium towards the end of May, and flies may be found fairly plentifully on the holly trees throughout June. Soon after fertilization the female proceeds to lay her eggs in the small young leaves of the current year's growth. This foliage, being quite soft, is easily penetrated by the ovipositor. The site selected for oviposition is located near the base of the mid-rib on the underside of the leaf. Here the female fly bores a vertical shaft which, on reaching the vessels of the leaf, bends at right angles and continues horizontally along the mid-rib. In this horizontal section of the tunnel the egg is deposited. The latter, which is white in colour and measures 0·383 by 0·160 mm., soon hatches, but for several months afterwards the small first-stage larva gives no indication of its presence in the leaf. During this period it remains hidden in the mid-rib, making its way slowly forward until in September, October or November, it leaves the central vessels and enters the soft green outer tissues. Here it gradually eats away the parenchyma below the epidermis until a large irregular blotch is formed. This blotch, or mine, which reaches its maximum size in March, may occupy a considerable area beneath either the upper or lower epidermis, but it is usually confined to the former, although occasionally it extends to both surfaces. Between July and March the larva moults twice and passes through three larval stages, the first lasting from July to December, the second from December to January, and the third from February until the formation of the puparium about the end of March. Some little time before pupating, the mature larva prepares a thin triangular area on the cuticle of the leaf, against which a hinged emergence plate of similar size on the puparium will abut, so that when the fly has matured, its escape may be easily accomplished. While feeding on the leaf-tissues, the larva lies on its side, but before entering the pupal stage it turns over on its back so that its ventral surface is pressed against the epidermis and its anterior spiracles are projected through the attenuated area of cuticle. The imago makes its escape from the leaf by pressing with the ptilinum against the hinged emergence plate on the puparium (fig. 2), which in turn breaks through the thin cuticle above it.

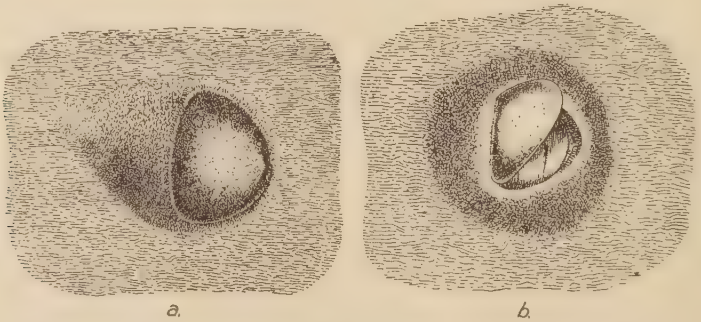

Fig. 2. Puparium of *Phytomyza ilicis* " in situ " on holly leaf; (*a*) before emergence of fly—note protruding anterior spiracles; (*b*) after emergence—note raised triangular flap (× 17).

In British Columbia, the life-history of the fly is substantially the same as it is in England, except that the emergence of the adults takes place about a fortnight earlier than in this country, and the other stages are correspondingly advanced.

Parasites of Phytomyza ilicis.

Although an extensive search was made through the literature only one previous record of a parasite of the Holly Leaf-miner in the Palaearctic region could be found, namely, *Dacnusa maculata*, Gour. (Braconid) on *P. ilicis* and *P. geniculata* in Italy (Leonardi 1922).[*] It may therefore be taken that the following species reared by the writer in the course of the present investigation are now recorded, from this host, for the first time.

CHALCIDOIDEA :

- Eulophidae :
  1. *Chrysocharis gemma* (Curt.) Walk.
  2. *Chrysocharis syma*, Walk.
  3. *Pleurotropis amyntas*, Walk.
  4. *Closterocerus trifasciatus*, Walk.
  5. *Tetracampe* sp. (near *nemocera*, Masi).
- Pteromalidae :
  6. *Sphegigaster flavicornis*, Walk.
  7. *Cyrtogaster vulgaris*, Walk.
  8. *Eutelus* sp. (near *dilectus*, Walk.)

ICHNEUMONOIDEA :

- Braconidae :
  9. *Opius ilicis*, Nixon.

Leonardi's species (*Dacnusa maculata*) was not obtained from English material.

The preceding parasites emerged from material collected mostly in the counties of Buckinghamshire and Surrey, while the commoner species were also obtained from the New Forest in Hampshire, and the Forest of Dean in Gloucestershire. The order of their abundance during the years 1937–38 was as follows : (1) *Chrysocharis gemma*, which was by far the most common species ; (2) *Sphegigaster flavicornis*, followed very closely and in some areas superseded by (3) *Chrysocharis syma* ; (4) *Cyrtogaster vulgaris* ; (5) *Pleurotropis amyntas* (4 and 5 were obtained in about equal numbers, but *P. amyntas*, on account of its hyperparasitic tendencies, is placed after *C. vulgaris*) ; (6) *Opius ilicis* ; and lastly, *Closterocerus trifasciatus* and *Tetracampe* sp., both of which were extremely rare. All of them, with the exception of *C. gemma*[†] which completes its life-history in the larva, are parasites of the pupa, and all except *P. amyntas* are primary in habit. The latter acts in the dual capacity of a primary on the fly pupa and a secondary on the larva and pupa of *Sphegigaster flavicornis* and other primary parasites.

After a detailed examination of the various developmental stages of the five most important Chalcid parasites of *P. ilicis* had been made, it was found that the larvae as well as the adults could be divided into two main groups, one consisting of the Eulophids—*Chrysocharis gemma*, *C. syma*, and *Pleurotropis amyntas*, all of which are endoparasitic in habit, and the other of the ectoparasitic Pteromalids, *Sphegigaster flavicornis* and *Cyrtogaster vulgaris*. This grouping was based on certain larval characters, which are enumerated and discussed in relation to the classification of Chalcid larvae, in Part IV of this paper. Because it has been found more convenient for descriptive purposes, the various parasites have been arranged in the text according to their position in these systematic groups, and not in the order of their abundance or importance as agents of control. *Chrysocharis gemma* has been made representative of Group I and *Sphegigaster flavicornis* of Group II, and these two species have been described in greater detail than any of the others.

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[*] The following five parasites were reared by Mr. F. W. Poos from *P. ilicis* in Virginia, U.S.A., some 3,000 miles from the present holly fly outbreak in British Columbia :—*Pleurotropis lithocolletidis*, Ashm., *Closterocerus tricinctus*, Ashm., *Sphegigaster* sp., *Herbertia* sp., *Opius striativentris*, Gahan. Specimens were kindly loaned to me by Mr. A. B. Gahan, of the U.S. Bureau of Entomology, for comparison with the English species. On examination, however, they were all found to be quite distinct from the latter. The possibility of utilizing them along with the English parasites in Western Canada will be discussed in a subsequent paper.

[†] *Opius ilicis* is a larval parasite in the first instar, but its later development is certainly completed in the host pupa.

The Braconid, *Opius ilicis*, Nixon, although not a common parasite of the Holly Leaf-miner, proved to be a new species and is therefore of more than usual interest. A separate paper dealing with the biology, etc., of this insect will appear at a later date. Because of this, only the briefest mention of it is made in these pages.

Key to Adult Parasites.

1. Antennae elbowed; wing venation simple, Chalcid type..............................2
   Antennae not elbowed; wing venation complex, forewing with only one recurrent nervure, Braconid type..*Opius ilicis.*
2. Fore tibiae with one large curved spine; marginal nerve shorter than the subcosta, radius usually long; tarsi five-jointed..3
   Fore tibiae with one short, thin, straight spine; marginal nerve mostly long, often longer but not shorter than the subcosta, radius and post-marginal usually short; tarsi four-jointed (except female of *Tetracampe* with five)...5
3. Abdomen sessile, legs yellow..*Eutelus* sp.
   Abdomen petiolated 4
4. Petiole longer than the hindmost coxae; legs medium brown.........*Sphegigaster flavicornis.*
   Petiole shorter than the hindmost coxae; legs almost black...*Cyrtogaster vulgaris.*
5. Wings with dark cross-bands..................................*Closterocerus trifasciatus.*
   Wings without cross-bands...6
6. Abdomen petiolated...7
   Abdomen sub-sessile 8
7. Antenna 10-segmented; tarsi with four joints, light-coloured, rest of leg dark... *Pleurotropis amyntas.*
   Antenna 12-segmented; tarsi of female with 5 joints, of male 4, dark-coloured like rest of leg...*Tetracampe* sp.
8. Femora pale straw-coloured; dorsum of female light green, of male burnished gold and green; scape of male yellow; dark circular area on forewings sometimes lighter in colour...*Chrysocharis gemma.*
   Femora black except for pale straw-coloured extremity; dorsum of female metallic green, of male dark bronze-green; scape of female black; dark circular area on forewings absent................................*Chrysocharis syma.*

Key to Primary Larvae.

1. Two stout projections forming a U-shaped marking on upper margin of mandibular bar..*Opius ilicis.*
   U-shaped marking not present on mandibular bar.......................................2
2. Antennae conspicuous; spiracles present on segments 2, 4, 5 and 6; tentorium well-developed; exceedingly minute spines on anterior margin of body segments 3

Antennae minute ; spiracles absent ; tentorium not apparent ; strong backwardly directed spines on segments 4 to 12 and a ring (somewhat incomplete) of similar spines on the posterior margin of segment 13................................4

3. The two species in this group are almost indistinguishable but the following characteristic may be of some value for identification purposes, although no guarantee of its invariability is given.

Two pairs of sub-labial papillae....................................*Cyrtogaster vulgaris.*

Sub-labial papillae wanting.......................................*Sphegigaster flavicornis.*

4. Head markedly quadrangular ; distal portion of mandibles (fig. 9 *c*) rather long, curved and narrow, base rather small ; contained within fly puparium, usually hyperparasitic...*Pleurotropis amyntas.*

Head thimble-shaped but more rounded than in preceding species ; mandibles (fig. 4 *c*) inverted L-shaped with large basal part ; primary parasite of the larva...*Chrysocharis gemma.*

As *C. gemma* but parasite of the pupa ; sub-labial spines more distinct than in preceding species and spines on posterior margin of segment 13 usually more abundant..*Chrysocharis syma.*

Key to Mature Larvae.

1. Skin smooth...2

Skin shagreened..*Opius ilicis.*

2. Tentorium very prominent ; atrium of spiracle large, diameter not less than 20 μ, rings below atrium 3–6 in number, valvular apparatus below rings conspicuous (fig. 13) ; endoparasitic type..3

Tentorium not apparent (if present, only weakly developed) ; atrium of spiracle less than 20 μ in diameter, rings below atrium 10–17 or more in number, valvular apparatus in spiracular trachea wanting (fig. 6)..........................4

3. The two species in this couplet are practically indistinguishable and the mature larvae should therefore be left for a few days until they have pupated, when identification becomes relatively easy..

Early pupa white in colour ; internal angle of antenna rounded (fig. 15 *d*)........ *Sphegigaster flavicornis.*

Early pupa white with black markings on venter of abdomen (fig. 15 *b*) ; internal angle of antenna sharp..*Cyrtogaster vulgaris.*

4. Larva or larval skin lying free in mine without any evidence of a puparium......... *Chrysocharis gemma.*

Larva contained in host puparium..5

5. Sensory papilla in region of inferior mandibular articulation vertical-oval in shape ; eight pairs of spiracles, the pair in 4th segment under-developed ; small rather slender larva, usually less than 2 mm. in length ; hibernates in larval stage and is usually hyperparasitic in habit.........*Pleurotropis amyntas.*

Sensory papilla more or less circular in outline ; seven pairs of spiracles ; larger larva, rather rotund, about 2·14 mm. in length ; does not hibernate as a larva and is primary in habit...................................*Chrysocharis syma.*

Key to Pupae.

1. Antennae longer than body and curved over dorsum of abdomen......*Opius ilicis.*

Antennae shorter than body...2

2. Colour shiny jet-black ; antennae joined to head in sub-ocular region ; cast skin black, hard, and retaining much of its original shape........................3

Colour matt-black, with dark brown appendages ; antennae joined to head near mid-ventral line ; cast skin tenuous, colourless and crumpled..................5

3. Pupa lying free in mine..*Chrysocharis gemma.*

Pupa in host puparium..4

4. Pupa with bulbous bow-shaped abdomen ; no remains of another parasite in host puparium..*Chrysocharis syma.*

Pupa with rather narrow abdomen and not as above ; remains of another parasite often found in host puparium.......................*Pleurotropis amyntas.*

5. Early pupa mostly white ; late pupa black, with dark brown appendages ; internal angle of antenna (fig. 15 *d*) rounded............*Sphegigaster flavicornis.*

Early pupa with striking black markings on ventral side of abdomen (fig. 15 *c*) ; late pupa black with dark brown appendages ; internal angle of antenna sharp..*Cytogaster vulgaris.*

1. **Chrysocharis gemma** (Curt.) Walk.

C. gemma is the commonest and most important parasite of the Holly Leaf-miner in the South of England. During the years under review (1937–38), some 30 to 40 per cent. of the fly larvae were found to have been attacked by this species in most districts, and in 1938 at Burnham Beeches in Buckinghamshire, a total of seventy-one out of a hundred hosts were parasitized by it. This was the maximum percentage of parasitism recorded for any parasite of *P. ilicis* during the course of the investigation.

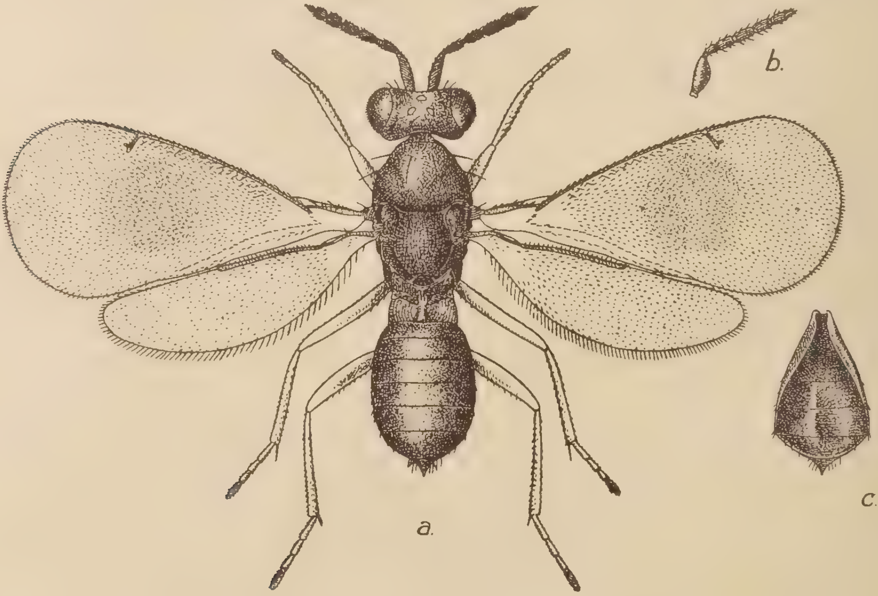

Fig. 3. *Chrysocharis gemma* : (*a*) adult female ; (*b*) antenna of male ; (*c*) shrunk abdomen of pinned female (× 24).

Distribution and Host Records.

The genus *Chrysocharis* is very widely distributed. It occurs in four out of the five continents of the world and has been recorded from the following countries :—

Europe : England, Germany, Austria, Spain, Sweden and Russia.

Africa : Kenya, Uganda and Tanganyika.

America : North and South America and Hawaii.

Australasia : New Zealand.

C. gemma itself has not been reared until now but was taken in Great Britain by Walker, who named the species. It was found to be common on *P. ilicis* in all the areas examined in the south-eastern counties of England, with the exception of Kew Gardens. Specimens were also obtained from holly material collected at Achterneed, Ross-shire, in the North of Scotland.

The host relationship of the genus, as revealed in the following list, which includes the four most important Orders of insects, is rather interesting.

Diptera : Mainly *Phytomyza* spp., also *Scaptomyza* and *Cerodonta* spp.

Lepidoptera : Mainly *Lithocolletis* spp., *Coleophora* spp., *Leucoptera* spp., and *Lyonetia* spp. (all Tineina).

Hymenoptera* : *Fenusa* sp., and *Phyllotoma* sp. (Tenthredinidae).

Coleoptera : *Rhynchaenus* spp. (Curculionidae).

Ashmead, the North American Chalcid expert, who was partly aware of this diversity of hosts, thought that many of the records were wrong and believed that most of the species would be found to be parasitic only on Diptera, since " where the records conflict", he says, " Diptera are usually associated with the Lepidoptera or Coleoptera either as parasites or as co-habitants on the same plant." The present writer, however, does not agree with this hypothesis because (1) most of the forty records examined appear to be perfectly genuine ; (2) the diversity of hosts is too great to be accounted for by mistakes in rearing ; and (3), most important of all, because all these hosts, although widely separated systematically, are closely linked ecologically. The larvae of all of them are leaf-miners, and being small and enclosed within the tissues of the leaf on which they feed, they present a more or less similar general appearance to the parasites which prey upon them.

General Biology of C. gemma.

The females of this species, in common with some of the other parasites of *Phytomyza ilicis*, have the rather unusual habit of overwintering in the adult stage. At first it was thought that they hibernated in some alternate host, but when they were found ovipositing in the mines very early in the year (end of February and beginning of March) doubts were entertained on this point. It was therefore decided that holly trees in the neighbourhood of the Laboratory should be swept at regular intervals throughout the winter months, especially on fine sunny days. As a result, females were taken from October onwards. Egg-laying begins towards the end of February and is general throughout March, while a small number of females may still be found attempting to oviposit early in April, although few host larvae are available at this late period. It is quite possible that in sheltered areas some eggs may be deposited at the beginning of February, or still earlier, if the weather is warm and the mines are beginning to show up, but the numbers laid before the end of this month must be very small indeed. The act of oviposition lasts about three minutes or less, a single egg being laid through the cuticle of the leaf and deposited in the body cavity of the larva. Occasionally a certain amount of superparasitism occurs, and two or more eggs may be found in the same host. In 1937, at Sunninghill, Berks., where this parasite was fairly abundant, eggs and first-stage larvae were

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* *Chrysocharis* sp. has been recorded both from an Ichneumonid, *Angitia* sp., and a Braconid, *Microgaster* sp., by Voukasovitch from Serbia, but in view of the fact that in all other records this genus is stated to be primary, it seems to me that these two instances of hyperparasitism are somewhat doubtful, and should be received with suspicion until further confirmation of them is forthcoming. It is quite possible that the real host, some inconspicuous leaf-miner on the same plant which harboured the host of these two parasites, had been overlooked.

quite common about the middle of March, and in 1938, owing to the advanced spring season, they were plentiful at the beginning of this month. Larvae which have been attacked by *C. gemma*, even although they contain only the egg of the parasite, are quite different in appearance from healthy unparasitized hosts. In contrast to the latter, which are rather turgid and of a bright, shiny lemon colour, they are flaccid and of a pale, dirty yellow hue. The incubation period lasts about a week to ten days, depending on the temperature, after which a very characteristic first-stage larva makes its appearance. The most striking peculiarity of this larva is the presence of backwardly projecting spines on segments 4 to 12, but these and other morphological characteristics will be discussed in a following section. From emergence to maturity some sixteen to twenty days elapse, during which time, so far as could be ascertained, the larva moults twice and passes through at least three distinct stages. (The difficulty of determining with any degree of accuracy the number of moults which an internal parasite undergoes in the course of its larval life, can easily be appreciated.) After feeding is completed, the larva remains in a resting stage for a further eight to ten days before it changes to a prepupa, so that altogether the duration of larval life is about four weeks, while the time spent in the prepupal and pupal stages is four and thirty-eight days respectively. Thus the total length of time occupied by metamorphosis, from the deposition of the egg to the emergence of the perfect insect, is roughly eighty-two days.

There is such a long period of egg-laying that eggs and all larval stages can be found throughout March and part of April. Pupae can be found from the 12th April onwards (or earlier if the spring is warm like that of 1938), and this instar becomes plentiful from about the second week in May. The imagos begin to make their appearance in June, the peak of emergence being reached about the middle of this month. As a rule the males emerge about five or six days before the females, and the sex ratio is 0·5 or two females to one male.

The mating habits of this species are rather unusual and therefore worthy of special notice. When the sexes are brought into close proximity the male becomes very excited, and with outstretched and rapidly vibrating wings and antennae, sets out in pursuit of the female. He approaches the latter from the side, and holds on to the dorsum of her thorax or a wing, with one of his anterior legs. In this curious position, with body held more or less at right angles to that of his mate, he keeps up a continuous vibration of wings and antennae. These preliminary manoeuvres, which are evidently intended to make the female receptive, last for several minutes, but the latter in captivity never appears to be much affected by them. Usually during their performance she busies herself in cleaning her abdomen with the posterior pair of legs and in moving her antennae slowly up and down. Often she gets tired of the whole business and walks away dragging the male after her, but when she stops he continues his antics as before, until meeting with no response, he eventually leaves her alone. Although the movements of several pairs were watched for some time, the consummation of this strange courtship was never observed in the Laboratory.

Description of Developmental Stages.

Egg.—The egg (fig. 4 *a*) is greyish white in colour, smooth and somewhat kidney-shaped. It is slightly broader at the anterior than at the posterior end, and measures 0·28 mm. in length by 0·084 mm. in maximum breadth.

First-stage Larva.—The first-stage larva (fig. 4 *c*) consists of a head and thirteen well-marked body segments. It is somewhat fusiform in shape and the skin is more or less transparent. When newly hatched it measures 0·29 to 0·31 mm. in length by 0·084 mm. in maximum breadth, the breadth of the head being 0·063 mm. The shape of the latter is somewhat like that of a thimble and bears quite a good general resemblance to that of the first-stage larva of many internal Ichneumonid parasites, such as for example, *Glypta haesitator*, etc. The mandibles are very distinct, and in side view the pharynx is clearly discernible. A distinct lobe is present on the ventral side of the head, some little distance behind the mouth. The skin armature, which consists of a row of small dorso-pleural spines (fig. 4 *c*) on the posterior margins of segments 4 to 12, is rather unusual. These measure about 2 to $2{\cdot}5\mu$ in length and are separated from each other by a similar distance, although they are not always regularly spaced in the row. The last segment, which is somewhat truncated, is characterized by a circular ring (incomplete ventrally) of strong spines on its posterior margin. On one occasion a first-instar larva of *C. gemma* was observed, through the more or less transparent skin of its host, to be moving along quite rapidly inside the body cavity of the latter. The method of propulsion involved the use of the spines, the truncated spiny thirteenth segment being placed against the tissues of the host and the body of the parasite by this means given a forward thrust. Perhaps some degree of discomfort experienced in the dissecting fluid caused the larva to move along in this manner, but at any rate the fact that it can move freely inside its host, when necessary, was clearly demonstrated. It is suggested that the aforementioned spines are mainly useful in effecting eclosion from the egg, a supposition which appears to be confirmed when one considers that they disappear after the first ecdysis. This point is discussed more fully in Part IV. The lay-out of the cephalic skeleton (fig. 4 *b*), or system of chitinized rods situated round the mouth, is very similar to that of the mature larva, so that a detailed description of it here will be unnecessary. Respiration in this stage is effected cutaneously, that is by diffusion of oxygen from the blood of the host. There are no spiracles, but very fine horizontal tracheal trunks partially filled with air may be traced in segments 2 to 7 or 8.

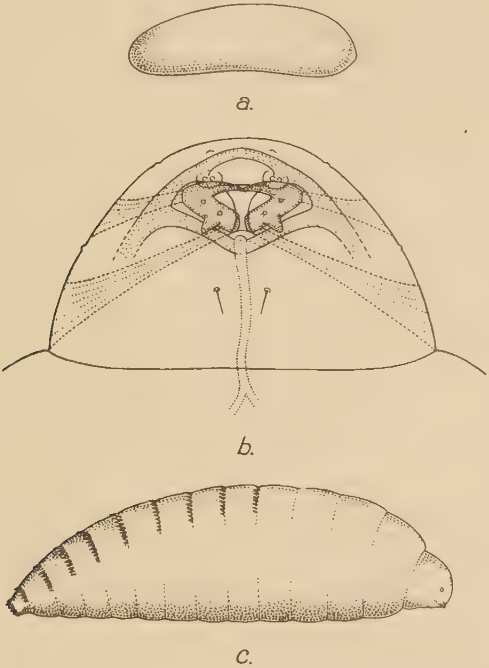

Fig. 4. *Chrysocharis gemma* : (*a*) egg (× 113) ; (*b*) head of first-stage larva showing cephalic skeleton and mandibular muscles (× 600) ; (*c*) first-stage larva (× 175)—note spines on segments 4 to 13.

The second instar may be distinguished from the first by the wider head (0·168 mm. compared with 0·105 mm.), the larger mandibles, and the absence of spines on the posterior segments of the body. Respiration in this stage is also apneustic.

Mature Larva.—The mature larva (fig. 7 *a*), like the primary one, consists of a head and thirteen body segments. It is somewhat fusiform in shape, whitish in colour, except for the dark faecal mass in the gut, which is visible through the body wall, and the skin is smooth and shiny. The larvae vary in size from 1·4 to 2·25 mm. in length, by 0·45 to 0·97 mm. in breadth, the larger individuals usually giving rise to female and the smaller to male imagos.

The head is differentiated into three lobes, two upper or epicranial, and a lower median or labial lobe. Situated on the two former are a pair of antennae which measure 18μ across at the base by 5μ in height. The cephalic skeleton (fig. 5) is rather characteristic, and in plan agrees very closely with that of the other internal Eulophid parasites of *P. ilicis*—*C. syma* and *Pleurotropis amyntas*. It is composed of the following parts :—a pair of inverted L-shaped mandibles, well chitinized at the tips ; two superior mandibular struts, each of which affords articulation to one side of a mandible ; the epistoma, a curved bar joining these two struts in the upper clypeal region, the pleurostoma consisting of two arms connecting the superior and inferior mandibular struts ; the inferior mandibular struts, each of which provides an articulating socket for the condyles on the other side of the mandibles (these inferior struts are joined together in the labial region of the mouth so that the compound structure appears like a U-shaped rod) ; and a vestigial hypostoma arising from the junction of the inferior mandibular strut and the pleurostoma. The large, well developed tentorium (fig. 12), which is such a prominent feature of the Pteromalid larvae described in this paper, is not apparent (if present at all it is only weakly developed) in the head of the Eulophid parasites of the Holly Leaf-miner. In addition to the foregoing chitinized rods, a number of softer structures are also associated with the cephalic skeleton. These are : the clypeus and labrum above the mouth, a pair of maxillae one on each side of it, the median labium below it, and the common salivary duct formed by the union of two smaller ducts, which opens into it in the labial region. A number of papillae or sensoria are situated on the head in the

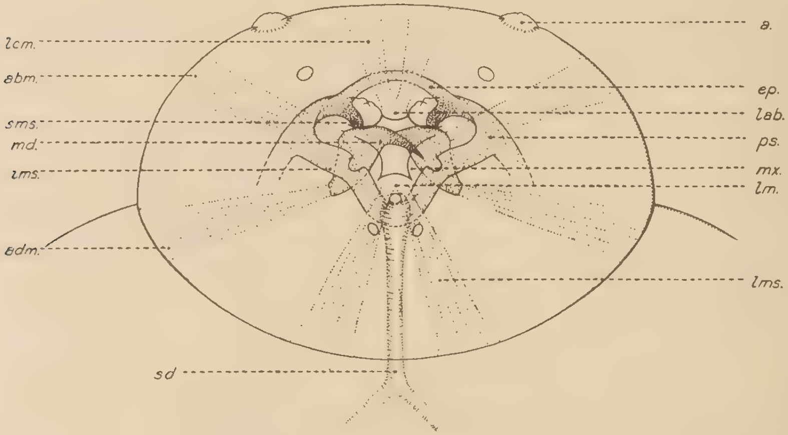

Fig. 5. *Chrysocharis gemma*, head of mature larva, showing cephalic skeleton (× 300) : *a*, antenna ; *ep*, epistoma ; *lab*, labrum ; *ps*, pleurostoma ; *mx*, maxilla ; *lm*, labium ; *lms*, labial muscles ; *lcm*, labro-clypeal muscles ; *abm*, abductor muscle of mandible ; *sms*, superior mandibular strut ; *md*, mandible ; *ims*, inferior mandibular strut ; *adm*, adductor muscle of mandible ; *sd*, salivary duct.

following regions : above the epistoma, and rather widely separated from each other, one rather large pair ; below the compound bar of the inferior mandibular struts in the sub-labial region and rather close together, a somewhat smaller pair, and two groups of three much smaller ones in the labial region. The main musculature of the cephalic skeleton (fig. 5) is composed of the following muscles—one set for the clypeus and the labrum, another for the labium, and two groups for the mandibles. The latter consist of two abductors, or opening muscles, attached to the upper part of the mandibles in the region of the right-angled bend, and two abductors attached to the base of the mandibles and serving to close them.

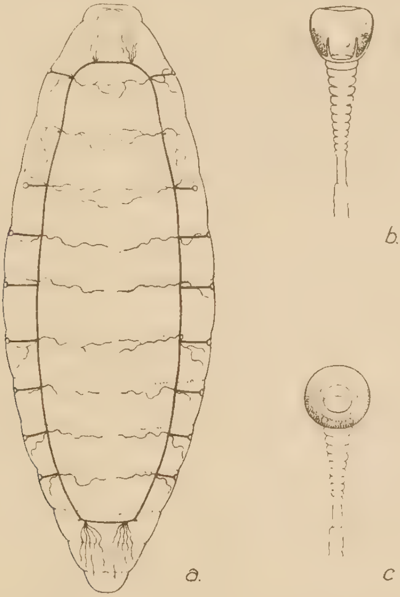

Fig. 6. *Chrysocharis gemma* : (*a*) mature larva (× 34), somewhat flattened, showing tracheal system ; (*b*) thoracic spiracle in side view ; (*c*) the same from above (*b* and *c* × 800).

The tracheal system (fig. 6) in this stage is peripneustic. It consists of two longitudinal trunks joined by transverse commissures in segments 2 and 11. From the anterior one, tracheoles are given off into the head region, and from the posterior, similar branches supply the last three segments. Spiracles are present on the anterior margins of segments 2 and 4 to 10, in all eight pairs. These are joined by short spiracular tracheae to the longitudinal trunks. From the junction of the spiracular tracheae and longitudinal trunks further tracheoles are emitted, which ramify in the various tissues of the body. The atrium of the spiracle (fig. 6 *b*) is somewhat quadrangular in shape, but the corners are rounded. It varies in size, but its average measurements in the abdominal region are as follows : maximum breadth 11μ, depth 7μ, diameter of opening 4μ. Those of the thorax are somewhat larger than those of the abdomen. All of these are characterized by a basal internal circle of short vertical rods. The spiracular trachea which joins the atrium to the main tracheal trunk is composed of about 12 to 17 rings, a short length of simple tubing with no sign of valvular apparatus, and a further piece of trachea with only very faintly defined constrictions. In the absence of a definite valvular apparatus in the spiracular trachea, like that, for example, of *Sphegigaster*, it is quite possible that the basal circle of chitinized rods within the atrium acts as a closing device.

Prepupa (fig. 7 *b*).—At the end of the resting stage mentioned in the account of the biology of this parasite, the mature larva becomes demarcated into three distinct regions: the head, composed of the old larval head with mandibles and cephalic skeleton still clearly discernible, and the first body segment; the thorax, composed of segments 2 and 3; and the abdomen, made up of the 10 remaining segments. Although the prepupal stadium might be said to occupy the time from cessation of feeding until the actual formation of the pupa, it is not until these regions are demarcated that the prepupa can be definitely identified. In this stage the faeces are voided and as a result the body becomes uniformly white in colour.

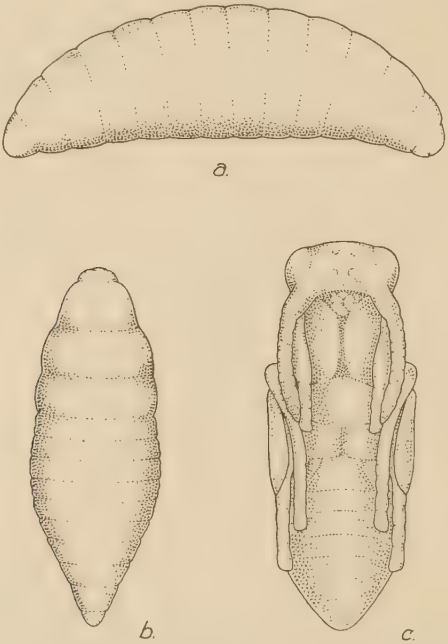

Fig. 7. *Chrysocharis gemma*: (*a*) mature larva; (*b*) prepupa; (*c*) pupa (× 34).

Pupa (fig. 7 *c*).—At first the colour of the pupa is pale yellowish-white, but this soon changes to a grey black and some time afterwards to a shiny jet-black. The various parts are well differentiated, wing and leg rudiments, eyes, mouth-appendages, as well as the thoracic and abdominal segmentation, being clearly marked. No cocoon is formed and the pupa lies free inside the mine. It varies in size from 2·60 to 1·75 mm. in length, by 1·04 to 0·65 mm. in breadth. The imago emerges from the leaf by a small neat round hole, which latter coupled with the small mine, the absence of a puparium, and the conspicuous black cast pupal skin left behind, enables one to identify very readily mines which have been occupied by this parasite.

2. **Chrysocharis syma,** Walk.

C. syma, which is a parasite of the pupa, is the third most important parasite of the Holly Leaf-miner. In 1938, during which year some 4,000 mined leaves, collected on sample twigs from twenty-one distinct and fairly widely separated areas, were examined, the parasitism of this species ranged from 0 to 13·8 per cent. (13·8 per cent. at Burnham Grove, Bucks.), whilst the average number of mines from which it emerged was 3·1 per cent. Because the amount of parasitism in each area is usually influenced by different sets of factors or by the same factors in differing degrees, and, in the case of the species which attack the pupa, is largely conditioned by the varying abundance or scarcity of previously acting agencies, such as larval parasites and predators, this latter figure is not intended to be a steady and absolute index of parasitism, but is only included here in order to give the reader a general impression of the relative abundance of the species concerned. Fuller data on this subject will be given in a paper dealing with the biological control of the Holly Leaf-miner.

Distribution and Host Records.

As already stated, the genus *Chrysocharis* has an exceedingly wide distribution, but *C. syma* itself has been taken only in England, Scotland and France. In the present investigation it was found to be fairly well distributed on the Holly Leaf-miner throughout the south-eastern counties of England, and a few specimens were obtained from the same host collected at Inverness in the north of Scotland. The only previous host records are those of De Gaulle (1908) from *Phytomyza geniculata* (France), and of the present writer (1935), who reared it from *Phytomyza atricornis*, Mg., a leaf-miner on *Senecio jacobaea*. De Gaulle does not give the host-plant of *P. geniculata*, but this species is known to attack both *Senecio jacobaea* and *Sonchus* sp. I understand that an associate of mine, Mr. F. Wilson, has also bred it from *P. atricornis* on *Lepidium draba* and from a leaf-miner on *Echium* sp., both in the south of France.

General Biology of C. syma.

The general biology of this species, when allowance has been made for the fact that it is a parasite of the pupa, is very similar to that of *C. gemma*. Eggs are laid internally in the fly pupae during April, or earlier if puparia are available (a number of mature larvae of this species have been found in early host puparia in February) and these hatch in from three to four days, according to the temperature. The development of the larva follows on the same lines as its congener, *C. gemma*. The prepupal and pupal stages last for 1½ and 19 days respectively, and adults make their appearance about the middle of June, while emergence is generally complete by the middle of July. Females are present in excess of males (144 females and 71 males obtained from samples in 1938), so the sex ratio is equal to 0·5. The preliminary courtship described for *C. gemma* is carried out in the same way by this species. One point worthy of notice in connexion with both *C. gemma* and *C. syma* is the way in which individuals of these species jump and hop about like fleas or plant-lice when they are approached or interfered with in any way.

Description of Developmental Stages.

Egg.—The egg is of a glassy white colour and is almost identical in shape and appearance with that of *C. gemma*. It measures 0·28 mm. in length by 0·08 mm. in maximum breadth.

First-stage Larva.—This instar is also very like that of *C. gemma*, in fact the two are so similar that it is extremely difficult to distinguish one from the other. Their relationship to the host, *C. syma* being a pupal parasite and *C. gemma* a parasite of the larva, provides the best clue to identification. Externally the larvae present the same general appearance, both being characterized by the posterior body spines described for *gemma*, and the only morphological difference that could be discerned was the trifling one, that the pair of long thin spines on the sub-labial region are much more distinct in the first stage larva of *syma* than they are in that of *gemma*, and the number of spines on the posterior margin of the 13th segment appears to be greater—32 compared with 12–15. Incidentally the first instar of *Pleurotropis amyntas*, the third endoparasite of *Phytomyza ilicis*, is also characterized by posterior body spines, and this is the only species with which *C. syma* is likely to be confused, but there are quite striking differences, especially in the head region, which can be used for separating the two larvae. These will be dealt with in the section assigned to *Pleurotropis*.

Mature larva.—The fully grown larva (fig. 8 *a*) is rather fat, rotund, somewhat fusiform in shape, and measures about 2·14 mm. in length by 0·97 mm. in maximum breadth. It is shiny, smooth and greyish white in colour with a central mass of black faeces and a large number of fat globules showing through the semi-transparent skin.

This instar can be distinguished from the corresponding stage in the other pupal parasites (with the exception of *Pleurotropis*) by its inconspicuous antennae, its greater rotundity, by the way in which the black bristles of the host usually adhere to it, and by the untidy condition of the puparium which it inhabits. If it is examined more closely and under greater magnification it will be seen that the tentorium (in Liquide de Faure mounts, see p. 205) as in *C. gemma* and *Pleurotropis amyntas*, and unlike the Pteromalids, is not apparent in the cephalic skeleton. The spiracles in the two groups are also quite distinct. In the endoparasitic Eulophids, of which group *Chrysocharis syma* is a member, the atrium is small and somewhat quadrate, whereas in *Sphegigaster*, etc., it is large and oval. The rings below the atrium in *C. syma* and the other members of its group are small and there are at least 10 to 17 of them, whereas in the Pteromalids they are large and not more than 3 to 6 in number. The conspicuous valvular apparatus in the spiracular trachea of *Sphegigaster* and *Cyrtogaster* is absent from *C. syma, C. gemma* and *P. amyntas*. Although it is relatively easy with these characteristics to separate the mature larva of *C. syma* from the larvae of the Pteromalid parasites of the puparium, it is much more difficult to distinguish it from that of its relative, *P. amyntas*, but there are certain differences which, though small, are useful for this purpose. For example, the two large papillae in the pleurostomal region are circular in outline in the larva of *C. syma*, whereas in that of *Pleurotropis* they are in the form of vertical ellipsoids. The hypostoma is also somewhat longer and more conspicuous in *Pleurotropis* than in *C. syma*, while the tracheal system, which in *C. syma* consists of 7 pairs of spiracles and in *P. amyntas* of 8 (undeveloped pair on segment 4), provides a further clue to identification. Again, the larvae of *C. syma* are all primary in habit, whereas those of *Pleurotropis* are, for the most part, secondary parasites and remains of the primary host can usually be found beside them. The majority of the larvae of the latter species also overwinter in the larval stage within the host puparium and no other parasite of the Holly Leaf-miner has this habit. These overwintering larvae, being hyperparasitic, are usually much smaller in size than the larvae of *C. syma* (2·14 mm. in length compared with 1·5 mm.).

Prepupa (fig. 8 *b*).—This stage in *C. syma* is very distinct. Like the mature larva it is characterized by great rotundity, but the most distinctive feature is the thorax, which with the head region (larval head and first body segment) occupies the anterior half of the body. These thoracic segments, which are very broad, smooth, shiny, and greatly distended, form a strong contrast to those of the prepupa of the Pteromalids, like, for instance, *Sphegigaster* (fig. 14 *b*), in which the segments of this region are narrow and more contracted, with deeply rounded sides. The more bulbous abdomen of *C. syma*, constituting the posterior half of the body and made up of the remaining ten segments, is also characteristic of this species. In colour the prepupa is yellowish and when newly formed it (female) measures 2·2 mm. in length by 0·84 mm. in breadth, but before entering the pupal stage it contracts so that its final measurements are 1·7 mm. by 0·8 mm.

Pupa (fig. 8 *c*).—At first the pupa is greyish black in colour, but a day after pupation it becomes quite black and shiny. It can be distinguished from the pupae of the other pupal parasites of *P. ilicis* by the bow-like shape of the body from the wing angle to the posterior segment of the abdomen. In the case of the Pteromalid pupae, the outer edge of the abdomen instead of being continuous with the wing margin, as in *Chrysocharis syma*, curves inwards underneath it. There is also a difference in the way in which the antennae are attached to the head. In *C. syma*, *C. gemma* and, to a lesser extent, in *Pleurotropis amyntas*, the basal part of the antenna is more or less undifferentiated and is attached to the head just below the eyes, whereas in *Sphegigaster* and *Cyrtogaster* this part is well segmented and its point of attachment lies near the mid-ventral line.

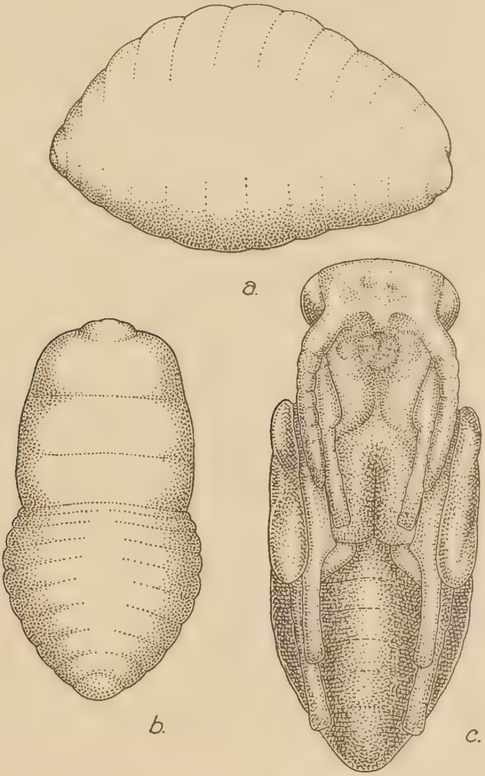

Fig. 8. *Chrysocharis syma*: (*a*) mature larva; (*b*) prepupa; (*c*) pupa (× 34).

3. **Pleurotropis amyntas,** Walk.

P. amyntas was found in the majority of areas where collections of mined holly leaves were made in south-east England, but it was never abundant. In 1938, the parasitism, calculated on the total number of mines examined, ranged from 0 to 1·5 per cent. (1·5 per cent. at Burnham Grove, Bucks.), whilst the general average was as low as 0·4 per cent.

This species is somewhat remarkable on account of its method of hibernating, the winter being passed in the mature larval stage within the host puparium, a habit shared by none of the other parasites of *P. ilicis*, and one that can be explained only on the ground of its hyperparasitic tendencies. As a result of a large number of dissections, and also of a certain amount of rearing work, it was definitely established that this species could act in the dual rôle of a primary parasite on the pupae of the holly fly itself, and of a secondary on the other pupal parasites of this host, such as *Sphegigaster flavicornis*, *Chrysocharis syma*, etc. When acting as a primary, development went forward in the normal way and adults emerged, along with those of the other primary species, in July. Apparently these adults then proceeded to parasitize the pupae of other parasites which were present in the puparia at that time, the resulting hyperparasitic larvae being found in August and throughout the winter.

Distribution and Host Records.

The genus *Pleurotropis* is a cosmopolitan one, with a wide distribution in Europe, America, Africa, Asia and Australasia. *P. amyntas* itself is known only from Britain, and no previous host record can be found in the literature, so that the present record from *P. ilicis* may be regarded as new. A history of hyperparasitism in this genus is well known. From a review of the literature it is evident that certain species are primary in habit, while others appear to be secondary, although the former are in the majority. It is quite possible, however, that many of the species, like the present one, are quite capable of acting either in a primary or a secondary capacity. As a rule *Pleurotropis* finds its hosts among Lepidoptera, Diptera (mostly AGROMYZIDAE), Coleoptera, and Hymenoptera. When reported as secondary, the hosts are said to be either Chalcids or Braconids.

General Biology of P. amyntas.

Adults emerge from overwintering larvae about the beginning of April (or towards the end of March in an early season like 1938). Mating was not observed to take place in the laboratory, but the preliminary courtship is similar to that of *C. gemma* and *C. syma*. In one experiment carried out in the spring of 1938 the same female laid eggs in the larvae of *Sphegigaster flavicornis* (fig. 9 *b*) and in the pupae of the fly itself. For the most part, however, adults which emerge from overwintering larvae appear to give rise to a brood of larvae which are primary in habit. These latter issue from the host puparia during July and apparently proceed to parasitize further puparia of *P. ilicis*, which now contain only pupae of parasites such as *Sphegigaster*, *C. syma*, and *Cyrtogaster* (all flies having emerged or been destroyed by some agency or other before this date). The secondary larvae thus produced have been found in the puparia from August onwards and they are smaller in size than the primary ones. These hibernating larvae enter the prepupal stage about the middle of March. After two days in this stage they become pupae, and remain as such for at least fifteen days longer (at 70°F.).

The sex ratio is 0·66, or 60 females to 40 males.

Description of Developmental Stages.

Egg.—The egg (fig. 9 *a*) is narrow, long and sub-reniform in shape and slightly longer than that of either *C. syma* or *C. gemma* (0·33 mm. cf. 0·28 mm.). It is smooth, white in colour, and measures 0·33 mm. in length by 0·08 mm. in breadth.

First-stage Larva.—The primary larva of *P. amyntas*, which when newly hatched measures 0·36 to 0·38 mm. in length by 0·09 in breadth, is very similar in many ways to that of both *C. gemma* and *C. syma*. It has the same fusiform shape, grey-white colour, and characteristic abdominal spines, but it can be distinguished from the first stage larva of the two latter species by the more or less quadrate head and long, narrow, pointed mandibles (fig. 9 *c*), which are quite distinct from the smaller inverted, L-shaped ones of *C. gemma* and *C. syma*. The sub-labial spines are also much stronger and more distinct in this species than in either of the two latter. In addition to these there are a number of small papillae, about five pairs in all, situated in various positions on the skin of the face. This instar differs from the corresponding one in the Pteromalids, *Sphegigaster* and *Cyrtogaster*, in the absence of spiracles and of a tentorium, both of which are so characteristic of these two species.

Mature Larva.—The mature larva (hibernating) is whitish in colour, with a dark central faecal mass and a large number of fat globules, averaging 0·10 mm. in diameter, showing up underneath the epidermis. Like the mature larva of the other Eulophids, it is smooth, somewhat shiny, and fusiform in shape, and measures, when normally extended, from 1·4 to 2·1 mm. in length by from 0·51 to 0·87 mm. in maximum breadth, the smaller larvae being the more common. As in *C. syma*, the only species with which it is likely to be confused, this stage differs from the mature larvae of the remaining parasites of *P. ilicis* in its inconspicuous antennae, weakly developed and inconspicuous tentorium, and the small, multi-ringed spiracles. The characters which enable one to separate it from *C. syma* have already been given in the section dealing with that species.

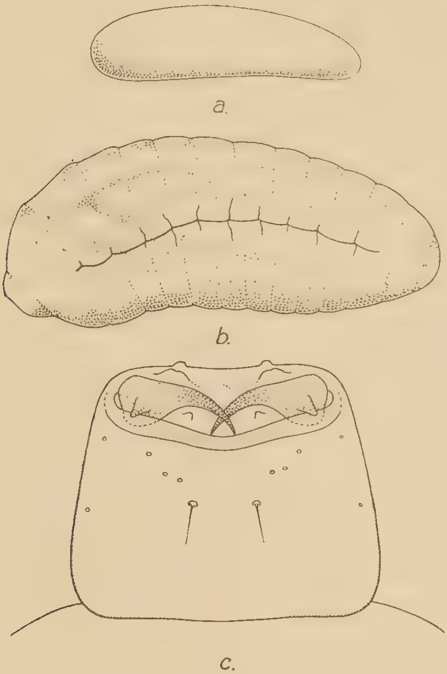

Fig. 9. *Pleurotropis amyntas*: (*a*) egg (× 113); (*b*) two eggs laid in first stage larva of *Sphegigaster flavicornis* (× 50); (*c*) head of first stage larva showing cephalic skeleton (× 450).

The tracheal system consists of eight pairs of spiracles, situated on the anterior margin of segments 2, and 4 to 10. The pair in the 4th segment, however, is usually incomplete, the spiracular trachea being very narrow and probably non-functional. There are ten to twelve rings on the spiracular trachea and a valvular apparatus in this part appears to be absent. The atrium of the thoracic spiracles is larger than those of the abdominal ones, measuring 17·3 μ in diameter, compared with 12·9 μ.

Prepupa.—The prepupa is white in colour and is divided into the usual three regions, head, thorax and abdomen. The thorax is very smooth and distended, while the abdomen is somewhat contracted and its segments are very narrow compared with those of the thorax. It can be distinguished quite easily from the Pteromalid prepupae by the inconspicuous antennae and the extreme distension of the anterior segments, and from that of *C. syma*, the only species with which it is likely to be confused, by its more tapering shape and smaller size. Length of male prepupa (from overwintering larva) 1 mm., maximum breadth 0·41 mm.

Pupa.—The newly formed pupa is mainly whitish in colour, except for small areas on the head, and the appendages which are dark grey. Soon after pupating the thorax and head become black, but the abdomen still remains whitish in colour, and continues like this for some time. About five days before the emergence of the imago, the whole pupa becomes quite black and shiny. The pupa of *Pleurotropis* can usually be recognised by the following characters—antennae attached to the head in the region of the eyes and not near the mid-ventral line as in the Pteromalids, abdomen comparatively narrow, especially when contrasted with the broad bow-shaped one of *C. syma*, and size rather small, measuring 1·12 to 1·55 mm. in length by 0·43 to 0·56 mm. in maximum breadth.

4. **Sphegigaster flavicornis,** Walk.

As already stated, *S. flavicornis* is the second most important parasite of *P. ilicis*. It is also the most common and most generally distributed pupal parasite of this insect. The average parasitism for the year 1938, based on the number of mines present on the sample twigs, was 4·5 per cent. and the range 0 to 16·6 per cent. (16·6 per cent. at Kew Gardens, Surrey). Because it is the chief Pteromalid parasite of the Holly Leaf-miner, it has been made representative of this group, and is therefore treated in greater detail than *Cyrtogaster vulgaris*, the other member of this Family.

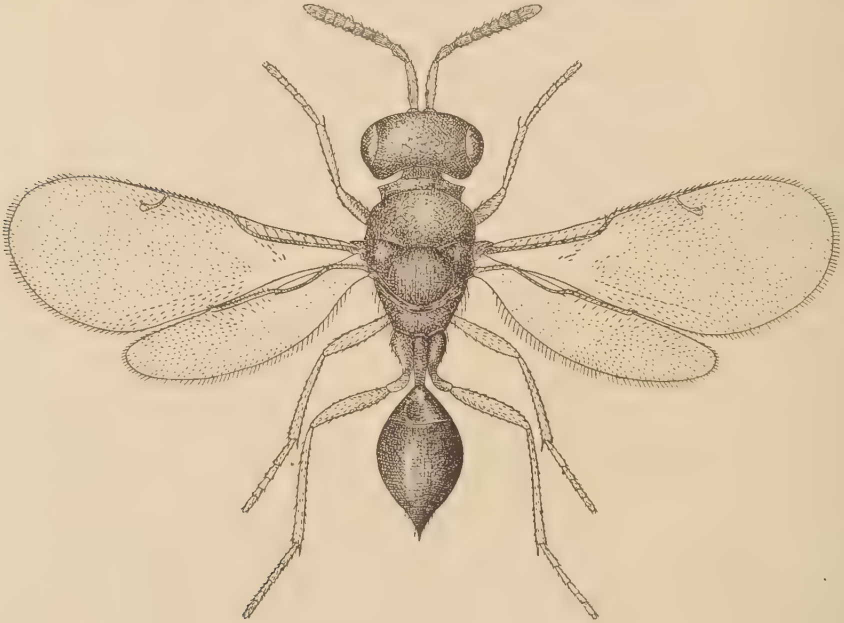

Fig. 10. *Sphegigaster flavicornis*, adult female (× 24).

Distribution and Host Records.

This species was found to be fairly well distributed in the holly areas examined in the south-east of England, and although no previous host record could be found in the literature, it has previously been taken on several occasions. Its geographical range, according to Schmiedeknecht, is North and Central Europe.

From the small number of host records available, it appears that members of the genus *Sphegigaster* for the most part parasitize leaf-mining and stem-boring Diptera, also gall-making species of the Family CECIDOMYIIDAE, while a few species attack Aphids.

General Biology of S. flavicornis.

This parasite becomes active on the holly tree about the beginning of April, and egg-laying by field-collected females was quite common in the laboratory from the 14th to the 26th of this month. The act of oviposition, which involves a good deal of boring through the cuticle of the leaf and the tough skin of the puparium, occupies a relatively long time, at least half an hour, and the egg is deposited externally on the pupa of the host. Incubation lasts for a period of 4 to 7 days, after which a typical first-stage larva—described in detail in the next section—makes its appearance, and proceeds to feed on its host from the outside. During the course of its larval life the skin is moulted four times, so that altogether there are five larval stadia. The larva is actively engaged in feeding for about 11 to 13 days and then enters a resting period lasting a further 4 to 5 days before it changes to a definite prepupa. It remains in the prepupal and pupal stages for two, and from five to six days respectively, before completing its metamorphosis and emerging as an imago about the middle of June. The peak of emergence is reached in the latter half of this month, but a number of individuals do not reach the adult stage until the earlier part of July, while in a few cases metamorphosis is not completed until the middle of August.

Males are slightly more numerous than females, but the sex ratio is almost equal to one (182 males to 161 females).

The mating, or at least the preliminary courtship, of *S. flavicornis* is quite different from that of *C. gemma* and the other Eulophids. When the male senses the presence of the female he vibrates his antennae violently and sways his body from side to side for a few seconds before setting off in pursuit. On catching up with her he mounts quickly, taking up a position well forward, with the first and second pair of legs clasped round her thorax and the third pair placed over her abdomen. He then, with a quick up and down movement, caresses her antennae, which are held pointing downwards, with his own. This lasts for a few seconds, and if the female is not sufficiently stimulated to desire copulation, he jumps off and moves away. He repeats this performance several times until she becomes receptive, when she bends up her abdomen slightly, he moves back, and copulation, which lasts for about ten seconds, is ultimately effected.

Description of Developmental Stages.

Egg (fig. 11 *a*).—The egg is glassy white in colour, and of a distinctive shape, somewhat arched, broad anteriorly, and tapering rather narrowly to the posterior end, while its chief characteristic is a narrow anterior nipple. It measures 0·34 mm. in length by 0·13 mm. in maximum breadth.

Primary Larva.—This stage (fig. 11 *b*) consists of a head and thirteen body segments. It is somewhat carrot-shaped, with a hemispherical head, broad thorax and tapering abdomen. The general body colour is glassy white, and the skin is more or less transparent. When newly hatched the larva measures 0·35 mm. in length by 0·13 mm. in maximum breadth. The head is characterized by a pair of conspicuous antennae and a strong cephalic skeleton, which will be described in more detail later on. A well developed tracheal system with four pairs of spiracles in segments 2, and 4 to 6, is a distinctive feature of this larva, as of the succeeding species, *Cyrtogaster vulgaris*. The skin of the body is characterized by a band of exceedingly minute spines on the anterior border of the segments, but there is no trace of large posterior spines, such as occur in the Eulophids, *C. gemma*, etc. The cephalic skeleton (fig. 11 *c*) is built on the same general plan as that of the preceding species, being complete with mandibles, epistoma, pleurostoma, hypostoma, mandibular struts, labium, labrum, and maxillae, with the notable exception that the tentorium (fig. 11 *c*) is now highly developed. In prepared slides, and in the figure, this structure is necessarily shown on the same plane as the rest of the mouth-parts, but actually in the living larva the long lower part from the bend (shown in the figure) projects into the head more or less at right angles to the main skeleton. In addition to the system of rods and soft structures around the mouth, there are a number of papillae on the surface of the skin, notably a group of three on each side of the head below the antennae, a pair just above the epistoma, and a third lot of three smaller ones on each side of the labrum.

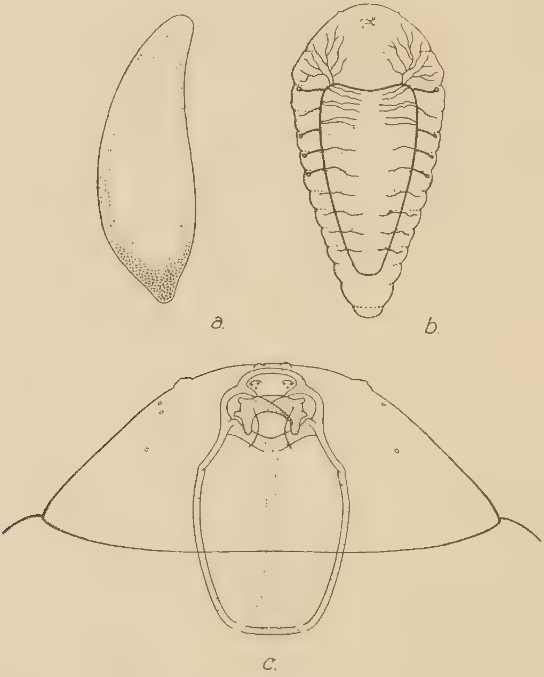

Fig. 11. *Sphegigaster flavicornis*: (*a*) egg (× 113); (*b*) first-stage larva showing tracheal system (× 113); (*c*) head of first-stage larva showing cephalic skeleton (× 450).

The primary larva of *S. flavicornis*, and also of *Cyrtogaster vulgaris*, the other Pteromalid parasite of *P. ilicis*, can be distinguished very readily from the corresponding instar in the Eulophids by the conspicuous antennae, the highly developed tentorium and the tracheal system complete with four pairs of functional spiracles. The difference between this larva and that of *Cyrtogaster* is extremely slight and will be found in the description of the latter species.

Mature Larva.—This stage is whitish in colour with a large brown internal faecal mass and fat globules showing through the semi-transparent skin. It is fat and flabby and fusiform in shape, the cuticle being smooth and devoid of spines. When normally extended it measures from 2·1 to 2·3 mm. in length by 0·92 to 0·97 mm. in maximum breadth. The head is somewhat hemispherical in shape and is characterized by a pair of very prominent antennae on the epicranial lobes. These are two-jointed, the basal one being large, with a diameter of 0·03 mm. and the terminal one rather small. The total length of the antenna is about 0·025 mm. As in the other species, the lay-out of the chitinized rods and associated structures forming the cephalic skeleton is based on a common plan, so that there is no need to describe these structures in detail, except in so far as they differ from the type—*C. gemma.*

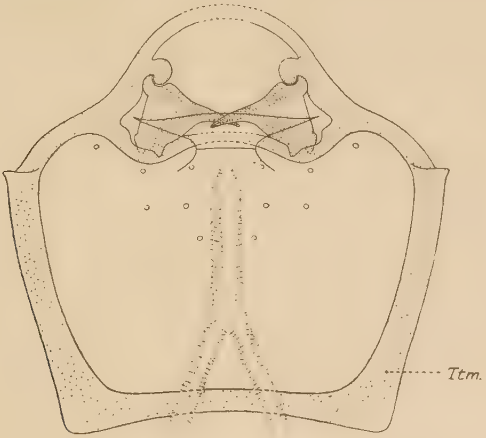

Fig. 12. *Sphegigaster flavicornis*, cephalic skeleton of mature larva: *Ttm*, tentorium (× 260).

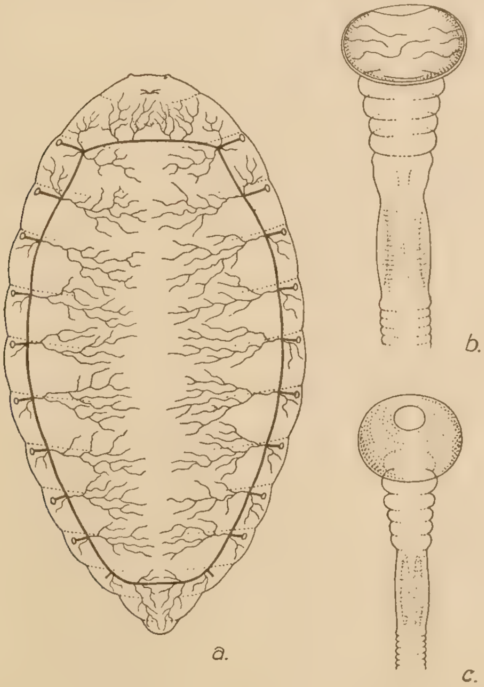

Fig. 13. *Sphegigaster flavicornis*: (*a*) mature larva (× 34), somewhat flattened, showing tracheal system; (*b*) thoracic spiracle in side view; (*c*) abdominal spiracle from above (*b* and *c* × 800).

In the cephalic skeleton of *Sphegigaster* (fig. 12) the most significant features are the large conspicuous tentorium, described for the first-stage larva, and the mandibles which are more triangular in shape, stronger and more workmanlike than those of the Eulophids. In contrast to the latter, the epistoma is very lightly chitinized and almost appears to be incomplete, especially in mounts which have been cleared. A fairly large number of papillae are scattered over the face of the mature larva of this species, especially in the sub-labial area (about twelve) and also in the epicranial region (one large pair).

The tracheal system (fig. 13) is very well defined. It consists of nine pairs of spiracles situated near the anterior margins of segments 2 to 10. These are linked up with two longitudinal trunks which are joined by transverse commissures in segments 2 and 11. From the main spiracular-longitudinal trunk junctions, ramifying tracheae and tracheoles carry a supply of air to the different organs of the body. All the spiracles are similar in shape and structure, but those on the first and second segments are somewhat larger than those on the remaining ones. The spiracle (fig. 13 *b*) is composed of a large ellipsoidal atrium with an average diameter of 23μ in the thoracic segments and 19μ in the abdominal, with a somewhat circular aperture 9μ and 6·5μ in diameter respectively. This is followed by a series of broad rings not more than six in number, and these in turn by a valvular tube with transverse and longitudinal striations. These large, well-constructed spiracles are similar to those of the other externally feeding larva, *Cyrtogaster vulgaris*, and are quite distinct from the small, multi-ringed, and apparently valveless type which are so characteristic of the mature larvae of the Eulophids.

Prepupa.—The prepupa of *Sphegigaster* (fig. 14 *b*), when newly formed, is whitish in colour with a yellow tinge. This stage is characterized by the old larval head with

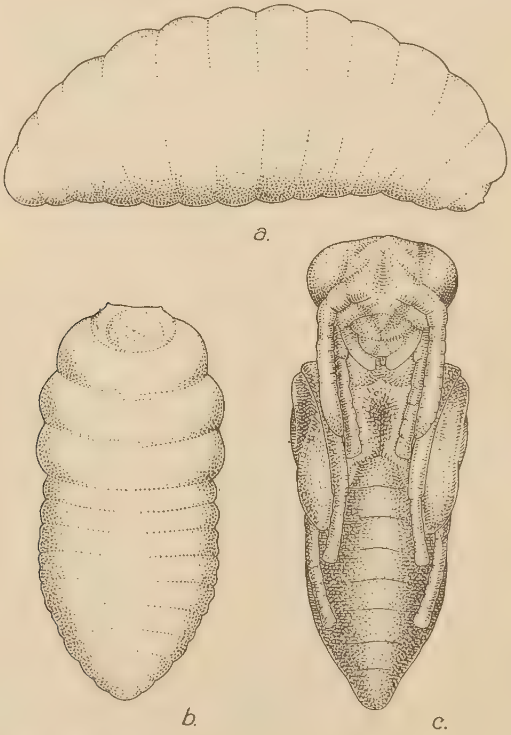

Fig. 14. *Sphegigaster flavicornis*: (*a*) mature larva; (*b*) prepupa; (*c*) pupa (× 34).

its conspicuous antennae, which along with the first body segment will form the head of the pupa and eventually of the adult, the two thoracic segments, which are large and stand out sharply from each other by means of the well rounded pleurae, and the abdomen which is constricted off from the thorax and consists of the remaining ten segments of the mature larva. The prepupa measures 1·95 mm. in length, by 0·73 mm. in maximum breadth.

Pupa.—At first the pupa (fig. 14 *c*) is white in colour, but in a few days the main part, with the exception of the antennae, wings and legs, which are of a light, glassy-brown hue, changes to black with a dull bluish tinge. The contrasting colour of the appendages and body gives a useful clue to the identification of this pupa. In the early stages it can be distinguished from the pupa of *Cyrtogaster*, the only one with which it is likely to be confused, by the absence of the black markings on the venter of the abdomen, which are so characteristic of the latter species, while after it has become darker in colour it can be separated from the other member of this group by the round internal angle of the antenna. Fuller details of these differences will be given in the section devoted to *Cyrtogaster*. The general colour, as described above, and the way in which the antennae arise from near the mid-ventral line of the head, enable one to distinguish it from the pupae of the three Eulophids, *Chrysocharis gemma*, *C. syma* and *Pleurotropis amyntas*.

5. **Cyrtogaster vulgaris,** Walk.

C. vulgaris is the second Pteromalid and the fourth most important parasite of *Phytomyza ilicis*. Like *Sphegigaster flavicornis* it attacks the host in the pupal stage. The average parasitism of this species in 1938 calculated on the total number of mines examined was 0·4 per cent. and the range 0 to 6·7 per cent. (6·7 per cent. at Hedgerley, Bucks.).

This Pteromalid, like the preceding one, belongs to the sub-tribe Sphegigasterini. It can be distinguished from *S. flavicornis* by the petiole, which in this case is shorter than the hind coxae, and by the colour of the legs which in *Cyrtogaster* are mainly black (in *Sphegigaster* they are medium brown). The globular distal end of the palpi is another very useful clue to the identity of the males of this species.

Distribution and Host Records.

C. vulgaris has been taken both in Europe and in America, but only three host records can be found in the literature, one from France on *Stilpnotia salicis*, the White Satin Moth which attacks poplar and willow, a second from Germany on a Dipterous fly, *Oscinella frit*, and a third, also from Germany, on a Braconid, *Coelinius niger*. To these may now be added the present one from England, on *P. ilicis*. Schmiedeknecht gives a list of fifteen species for this genus, most of which have been taken and named by Walker in Britain and a few by Ashmead in America. In the Farnham House catalogue only six host records are listed. These are (1) *C. glasgowi* from *Brachydeutera argentata* (Ephydrid), (2) *C. liqueatus* from *Phytomyza delphiniae* (Agromyzid), (3) *C. occidentalis* from *Cerodonta dorsalis* (Agromyzid), all three from the U.S.A., the remaining three being those mentioned above from France and Germany. In view of the fact that five of these records (including my own) state *Cyrtogaster* to be a primary parasite on Dipterous puparia, it would perhaps be better to regard the German record (*C. vulgaris* as a secondary on the Braconid *Coelinius niger*) with some suspicion, at any rate until further evidence of a hyperparasitic tendency in this genus is forthcoming.

General Biology of C. vulgaris.

The life-history of this species is in most respects similar to that of *Sphegigaster flavicornis*, so that an account here would mean unnecessary duplication. Two points of interest may, however, be mentioned, (1) that females of *C. vulgaris* lived right through the winter in the laboratory (first noted by Mr. L. R. Finlayson of Belleville in material sent over to Canada by the author), and a new generation was reared from them in the following spring ; and (2), that a remarkable characteristic of this species is its ability to feign death. This is so strong and real that, unless the observer is aware of this habit, he will be completely deceived.

The sex ratio is 0·5 or two females to one male, and the species is primary and solitary in habit.

Description of Developmental Stages.

Egg.—The egg of *Cyrtogaster* (fig. 15 *a*) is dull greyish-white in colour and is very similar in shape to that of *S. flavicornis.* It measures 0·38 mm. in length by 0·105 mm. in maximum breadth.

Primary Larva.—This stage is almost a replica of the corresponding instar in *S. flavicornis.* The only difference that was observed was that in *Cyrtogaster* two pairs of papillae were present in the sub-labial area, and these were absent from this region in the larva of *Sphegigaster.*

Mature Larva.—This stage again resembles that of *Sphegigaster* so closely that it is extremely difficult, if not impossible, to separate the two. The only method of distinguishing between them that could be adopted was that of allowing the larvae to pupate, when, both in the early and late pupae, useful characteristics were found which admitted of relatively easy identification.

Prepupa and Pupa.—The prepupa is similar to that of *Sphegigaster*, but quite appreciable differences can be made out in the pupa. When newly formed the latter is mainly white in colour, save for certain striking black markings on the venter of

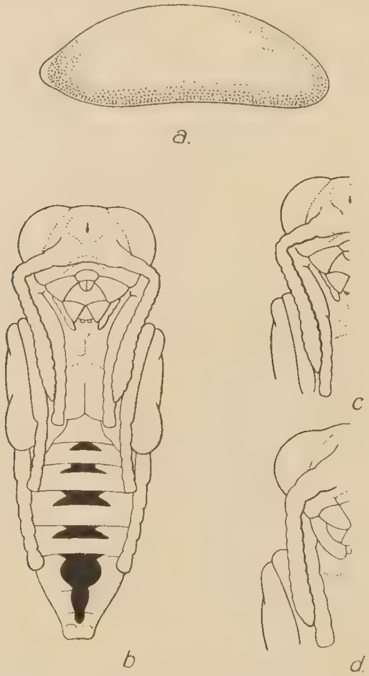

Fig. 15. *Cyrtogaster vulgaris*: (*a*) egg (× 113) ; (*b*) early pupa with characteristic black markings on venter of abdomen ; (*c*) view of antenna for comparison with that of (*d*) *Sphegigaster flavicornis* (*b*, *c*, and *d* × 34.)

the abdomen (fig. 15 *b*). These dark areas are sufficient to separate the early pupa of *Cyrtogaster* from that of *Sphegigaster*, which is entirely white in colour. Another very useful characteristic is the internal angle of the antenna (fig. 15 *c*); which in *Cyrtogaster* is sharp and in *Sphegigaster* rounded, a point which can be better appreciated if reference is made to fig. 15 *c* and *d*. After a few days the white areas of the pupa begin to darken and ultimately become black in colour, except for the wings and appendages, which take on a dark smoky-brown hue. On the whole the pupa of *Cyrtogaster* appears to be somewhat more shiny than that of *Sphegigaster*, which latter has more of a matt appearance.

6. **Opius ilicis,** Nixon.

This pupal parasite was reared from only three areas—Farnham Royal, Bucks.; Sunninghill, Berks.; and the New Forest, Hampshire. It is quite possible that it occurs elsewhere, but being comparatively rare, large numbers of puparia would have to be collected in order to get further examples. In 1938 an average of only 0·3 per cent. of the mines were attacked by this species. Specimens of the imago were submitted to the systematists of the Imperial Institute of Entomology for identification. Mr. Nixon, of that Institution, found that the species was new, and his description of it has already been published (Ent. Mon. Mag. **75,** 1939, p. 80). My account of the biology of this interesting parasite will be published in a separate paper at a later date. All that need be said about it here is that the various developmental stages can easily be distinguished from the corresponding instars of the Chalcid parasites of *P. ilicis*, the adult by the Braconid type of venation and the long straight antennae, the mature larva and prepupa by the dense covering of cuticular spines, which gives these two stages a shagreened appearance, and the pupa by the long antennae which extend down over the ventral surface of the body and curve back over the dorsum of the abdomen.

7. Rare Parasites of Phytomyza ilicis.*

A few specimens of the following rare pupal parasites were reared during the course of the investigation:—*Closterocerus trifasciatus*, Walk., *Tetracampe* sp. near *nemocera* and *Eutelus* sp. near *dilectus*. The two latter species are probably new to science.

Notes on the Morphology and Classification of Chalcid Larvae.

Before proceeding to an examination of the characters which have been found of some value in separating the Chalcid larvae parasitic on *P. ilicis* into different groups, it may be as well at this point to give a brief explanation of the origin of the terminology employed in describing the various structures of the head region. The term *cephalic skeleton* has been coined by the author to denote the system of chitinized rods which is found in the head (and usually grouped around the buccal region) of most parasitic larvae belonging to the families ICHNEUMONIDAE, BRACONIDAE and CHALCIDIDAE, etc., whilst the names of the different parts of this skeleton are chiefly those originated by Thorpe (formerly of this Laboratory), who first used them in his paper on the Ichneumonid parasites of the pine shoot moth, *Rhyacionia buoliana* (1930). In 1933 Vance & Smith drew up a generalized system of nomenclature for these structures, but with the exception of their terms—*epistoma*, *pleurostoma* and *hypostoma*, which are more illuminating than the corresponding ones of Thorpe, I prefer to adhere to the original names. One or two modifications have been introduced by the present writer in previous papers (1935, 1937 and 1938) and two of these are repeated here, namely the terms—*superior* and *inferior mandibular struts*, in place of Thorpe's labral and mandibular struts. This has been done because the relation of these parts to the mandibles, and also their position in the cephalic skeleton, is better established by this terminology. The author agrees with Vance & Smith in their definition of the *tentorium*, which word should be preserved for the internal supporting structure of the head (fig. 12, *ttm.*), and should not be used inclusively, as it was by Thorpe, for the labral, mandibular, maxillary and labial struts, etc.

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* One or two specimens of *Eutelus* sp. and *Entedon* sp. were recovered from the very large collections of mined holly leaves (over 100,000 in 1938) after they had arrived in Canada. From the information to hand, however, it is not absolutely certain whether these species really are parasitic on *P. ilicis*. If so, they must be very uncommon.

The external morphology of Chalcid larvae is similar in many respects to that of the corresponding stages in the Ichneumonids and Braconids, but as a rule the parts of the cephalic skeleton, and consequently the characters which can be used for systematic purposes, are fewer in number. For example, the maxillary and labial struts, labial ring, clypeal arch, etc., are wanting in this group. Nevertheless, certain characteristics such as, general shape, size of antennae, composition of cephalic skeleton (including the shape of the mandibles), method of respiration, form of the spiracles, and the nature of the skin armature, can be usefully employed for separating the various larvae into distinct and homogeneous groups. Quite striking differences in these structures have been observed in both the primary and the mature larvae of *P. ilicis*, and it is on this basis that they have been divided into the two following classes :—(1) the *Chrysocharis* group, consisting of *Chrysocharis gemma*, *C. syma* and *Pleurotropis amyntas* ; and (2) the *Sphegigaster* group, which includes *Sphegigaster flavicornis* and *Cyrtogaster vulgaris*. The distinctive characteristics of each division are tabulated as follows :—

TABLE I.

Primary Larvae.

Characters	*Chrysocharis* group	*Sphegigaster* group
Shape ...	Head somewhat thimble-shaped, especially in *Pleurotropis*, body cylindrical and somewhat pointed posteriorly (fig. 4 *c*). Head and 13 body segments, including "tail" segment.	Head semi-spherical, body carrot-shaped (fig. 11 *b*). Head and 13 body segments.
Antennae ...	Minute.	Well-developed.
Cephalic skeleton ...	Tentorium not apparent (fig. 4 *b*). Mandibles somewhat comma-shaped, with distal end more developed in *Pleurotropis*.	Tentorium very conspicuous (fig. 11 *c*). Mandibles somewhat more triangular, with large lower condyle.
Respiration ...	Apneustic.	Peripneustic.
Spiracles ...	Absent.	Four pairs situated on segments 2, 4, 5 and 6 (fig. 11 *b*).
Skin armature	Strong backwardly directed spines on segments 4 to 12, last segment truncated with a ring of spines on the posterior margin (fig. 4 *c*).	Segments banded anteriorly with exceedingly minute spines ; large posterior spines wanting (fig. 11 *b*).
Mode of life ...	Endoparasitic.	Ectoparasitic.

TABLE II.

Mature Larvae.

Characters	*Chrysocharis* group	*Sphegigaster* group
Antennae ...	Rather small (length in *C. gemma* 5μ, diameter base 18μ).	Very prominent (length in *S. flavicornis* 0·025 mm., diameter base 0·03 mm.).
Cephalic skeleton ...	Tentorium not apparent, if present only very weakly developed. Mandibles (fig. 5) inverted L-shaped.	Tentorium (fig. 12) strong and very conspicuous. Mandibles triangular.
Respiration ...	Peripneustic.	Peripneustic.
Spiracles ...	Small, multi-ringed. No valvular apparatus in spiracular trachea (fig. 6), seven or eight pairs present on segments 2, and 4 to 10. In *Pleurotropis* those in segment 4 are under-developed and are probably non-functional.	Large, not more than six rings below the atrium. Distinct valvular apparatus in spiracular tracheae, nine present on segments 2 to 10 (fig. 13) ; all functional.

In addition to the differences which have been observed in the primary and mature stages of the larvae, further points of systematic value which emphasize the homogeneity and distinctiveness of each group can be found in the eggs, prepupae and pupae. For example, the *Chrysocharis* type of egg (fig. 4 *a*) is a little broader at the anterior than at the posterior end ; both ends are rounded and the lower border is slightly concave. In *Sphegigaster* and *Cyrtogaster*, on the other hand, the egg (fig. 11 *a*) is much broader anteriorly and tapers rather narrowly to the posterior end, whilst its most characteristic feature is a conspicuous anterior nipple.

In the prepupae of the first group, as in the larvae, the antennae are inconspicuous, while in the second they are very prominent. Again, in group (1), the first three body segments are rather distended, whereas in group (2) they are more contracted, with well-rounded pleurae and rather deep inter-segmental constrictions. The pupae of the two groups are also quite distinct. Those of the former are characterized by a shiny jet-black colour, whilst those of the latter, although also largely black, have more of a matt appearance, and the appendages are dark brown. Another distinction between the pupae of the two groups is to be found in the manner of attachment of the antennae. In *Chrysocharis* and its allies these are joined to the head in the sub-ocular region, whereas those of *Sphegigaster* are attached to the central area of the face.

Further useful differences can be detected in the host cocoon from which the respective parasites have emerged. Those of the *Sphegigaster* group are usually very clean and tidy, while the pupal skin, which has been deposited in a neat bundle along with the faeces and larval exuviae at one end of the puparium, is rather tenuous, crumpled and colourless. In *C. syma* and *P. amyntas*, on the other hand, the host cocoon is always untidy and the large black pupal skin, which retains something of its original shape, is the most prominent object in the puparium, as it is in the vacated mine of *C. gemma*. Salt (1931) found a similar type of pupal skin in *Pleurotropis benefica*, a parasite of the wheat-stem sawfly, *Cephus pygmaeus*.

We shall now proceed to compare the systematic findings which have been obtained in the present investigation with the results of other workers in this field. The papers dealing with the immature stages of the CHALCIDIDAE are few in number, and perhaps the best known and most comprehensive is that of Parker (1924). This author after examining a great deal of material came to the conclusion that his larvae could be divided into seven broad general groups. In order that the reader may get a "bird's-eye view" of the present state of the classification of Chalcid larvae, the latter, with the exception of groups 2 and 5, which are given in full for purposes of comparison, are reproduced here in abbreviated form.

1. Primary larvae almost spherical, etc., etc., *Aphelinus* spp. (see Imms (1918) for good examples of this group).
2. Cylindrical larvae with large antennae. This group is described in greater detail in a succeeding paragraph.
3. Larvae of polyembryonic Encyrtids. Mandibles, sensoria and spiracles absent. *Copidosoma, Litomastix*, etc.
4. Ovoid larvae with only ten distinct body segments as compared with the usual thirteen. *Blastothrix, Aphycus*, etc.
5. Ichneumoniform type. This group is also described in greater detail in a succeeding paragraph.
6. Larvae with very strongly chitinized head, chestnut-coloured, hairy, etc. *Eurytoma*, etc.
7. Larva in form of a planidium. Dorsal surface of body chitinized and composed of strongly pigmented plates. *Perilampus, Schizaspidia*, etc.

The two groups described in the present paper correspond most closely with Parker's groups 2 and 5—*Chrysocharis* with 5 and *Sphegigaster* with 2. In order that a comparison may be made between them Parker's description of these two classes (translated from the French) will now be given in more detail.

Group 5. *Corresponding with the* Chrysocharis *Group.*

Primary Larvae.

"The form of the larvae in this group is very characteristic. They resemble in a general way the primary larvae of certain Ichneumonids which have been called 'larves Ichneumoniformes.' The larvae of *Chalcis, Aspidiotiphagus, Cerapterocerus* and *Tetrastichus* are of this type. They are composed of a head and twelve clearly marked body segments followed by a short pointed tail. The head is longer than broad, shaped like a thimble, white in colour, and lightly chitinized; the sensorial organs of the head are little developed and, except in the larvae of *Chalcis*, antennae appear to be wanting. The mandibles are much arched and comma-shaped. In *Chalcis* each segment is surrounded by a band of small pointed spines, in *Tetrastichus* there is a row of spines on the posterior border of the segments . . . . . at the extremity of the tail there is a series of large spines . . . . all the larvae of this group are apneustic."

Changes in Mature Larvae.

"The spines and tail have disappeared and the head has become more spherical; except in *Aspidiotiphagus*, which retains the same sharp curved mandibles of the primary stage, these organs are more triangular in shape. There are nine pairs of open spiracles. The antennae are better differentiated than in the first stage, the sensoria on the head are more numerous and the tentorium is trapezoidal . . . ."

If the foregoing descriptions be compared with those of the *Chrysocharis* group in Table I, it will be seen at once that there is a high degree of correspondence between them. As for the term Ichneumoniform larva, the author when examining the primary stage of *Chrysocharis*, etc., was immediately struck by the close resemblance between the head of this larva and that of certain first instar endoparasitic Ichneumonids on which he was working at the time, e.g., *Glypta haesitator*, etc. Although the posterior part of the body is rather pointed, the tail, which usually accompanies this type of head in the latter group, is not distinct. This deficiency, however, does not prevent these larvae from being included in the Ichneumoniform class, as the general resemblance between the primary larvae of the two groups, especially of the head, is too strong. Nor did it deter Parker from placing *Tetrastichus*, in which the tail is also undifferentiated, in this division. Parker's group 5 and my *Chrysocharis* group (primary larvae) further correspond to each other in the matter of skin armature, including the posterior circle of spines in the last segment, and also in the apneustic type of respiration. The presence, or absence, or degree of development of a tentorium, which Parker does not mention here, will be discussed in a later paragraph. As far as the mature larvae are concerned the similarity is also quite marked. Evidently the mandibles of *Aspidiotiphagus*, which are of the primary type, are an exception in Parker's group, but both *Chrysocharis* spp. and *Pleurotropis* have inverted L-shaped mandibles, almost identical in shape with those of the first-instar larva. Again, Parker postulates nine pairs of spiracles in the mature larva, but in both *Chrysocharis* and *Pleurotropis* there are not more than eight pairs. Taken as a whole, however, there can be no doubt that the two groups are one and the same.

Group 2. Corresponding with the Sphegigaster *Group.*

Primary Larvae.

" This group includes the great majority of Chalcid larvae (*Melittobia*, *Dibrachys*, *Megastigmus*, etc., etc.). It is characterized by the cylindrical form of the body which is a little tapered posteriorly. The larva consists of a head and thirteen body segments. The head, which is as broad as the thorax, white in colour, and moderately chitinized, bears a pair of antennae which are longer than broad, and several sensoria ; the mandibles are very pointed, a little arched and simple. Each segment of the body bears on the anterior border a band of very minute spines visible only under the strongest magnification ; the thoracic segments each possess three pairs of sensorial tubercules . . . . . and the abdominal ones, except the last, two pairs. The respiratory system includes four pairs of open spiracles situated on segments 2, 4, 5, and 6. . . . . . ."

Changes in Mature Larvae.

" In this stage the arched mandibles are replaced by more triangular ones. The minute spines on the body segments have disappeared. Except in *Archirileyia*, there are five supplementary pairs of open spiracles. The tentorium which was formerly circular in outline is now trapezoidal . . . . . "

Again, if a comparison be made, it will be seen that there is a great similarity between Parker's group 2 and my *Sphegigaster* group. The main difference is to be found in the tentorium (figs. 11 and 12), which in the latter group is more or less trapezoidal (not circular) in the first as well as in the last instar.

Although he gives a good account of the tracheal system in general, Parker does not appear to have examined the spiracles very closely or, at any rate, he does not make use of them as an aid to classification, yet I have found them to be of great value for systematic purposes both in the Chalcid parasites of *P. ilicis* and in the Ichneumonid larvae parasitic on the spruce sawfly, *Diprion polytomum* (Morris, Cameron & Jepson, 1937), etc., etc. This author states that there are nine pairs of open spiracles in the mature Chalcid larva (*Aphelinus* and *Archirileyia* apparently excepted), a statement which is certainly true of the members of the *Sphegigaster* group but not of *Chrysocharis* and its allies. In *C. syma* there are only seven pairs, in *C. gemma* there are eight, and in *Pleurotropis amyntas*, in which there are the same number, the pair on the fourth body segment is only weakly developed and is almost certainly non-functional. This latter example contradicts Parker's statement that " the spiracles are always open." If reference be made to the description of the spiracle of *Sphegigaster* (p. 196) it will be seen that a closing device, or at any rate some structure which is exceedingly like one, is present in the spiracular tracheae, while a ring of spines is shown at the base of the atrium of *Chrysocharis gemma* (fig. 6 *b*), for which a regulative function is suggested. These examples are also in direct contradiction to Parker's statement that " the spiracles . . . . . do not possess a closing apparatus."

A word remains to be said about the tentorium, that structure which supports the cephalic skeleton from the rear. In the CHALCIDIDAE it usually consists of a single rod joining each end of the hypostoma, and the dorsal arms, which are present in many ICHNEUMONIDAE, are apparently wanting. This rod in the primary larvae may either be straight (as in *Chalcis*, etc.), semi-circular (as in *Microplectron*, etc.), or trapezoidal (as in *Sphegigaster*, etc.), or it may be vestigial or absent (as in *Chrysocharis* and *Perilampus*, etc.). When examining mounts (Liquide de Faure, see p. 205) of the Chalcid larvae described in this paper under the microscope, the strong well developed tentorium (fig. 12) of the members of the *Sphegigaster* group was usually the first thing that attracted my attention, and its apparent absence in both *Chrysocharis* spp. and *Pleurotropis* afforded a quick and easily observed distinction between the two groups. (Traces of a weakly developed tentorium in the mature larvae of *Pleurotropis*, etc., can be made out with difficulty in stained specimens.) Parker found this organ in the majority of the larvae which he examined, with the exception of the primary larvae of *Perilampus* and *Aspidiotiphagus*, the mature larva of an unknown Eulophid parasite of a big Coccid, and the mature larva of *Perilampus*, in which he could not see the longitudinal arms ; while Salt, in his study of the parasites of the wheat-stem sawfly, was unable to find a trace of it in the larva of *Pleurotropis benefica*. In the parasites of *P. ilicis*, as already pointed out, it is an important diagnostic character and the writer is convinced that, when a greater number of larvae have been examined, the degree of development of this structure will provide a useful clue to the identification of certain sub-divisions in the main scheme of classification.

When the comparatively small numbers of larvae which have been examined thus far have been considered, it will be realised that any system of classification of Chalcid larvae which is put forward must of necessity be very incomplete. Nevertheless, Parker's seven groups, and especially 2 and 5, which have been verified and somewhat modified as a result of the present study, appear to be sound enough to provide a good foundation for future workers in this field.

With regard to the relationship between larval and adult classification, it will be seen that there is a certain amount of correspondence between the two systems ; for example, all the members of the *Chrysocharis* group belong to the family EULOPHIDAE, and those of the *Sphegigaster* group to the PTEROMALIDAE ; but it is extremely doubtful if this degree of correlation will be found general throughout the CHALCIDIDAE. Indeed, Parker, although he found certain similarities between the grouping of his larvae and that of the adults, found also a good deal of overlapping. It seems to me that the characters which I have described in the preceding pages are more related to the mode of life of the larva than to the present system of adult classification. For example, the antennae would appear to be more useful to the primary larva of an external feeder like *Sphegigaster* than to the corresponding instar of a submerged endoparasite, like *Chrysocharis*. There is also a possibility that the egg of *Sphegigaster*, because of its shape, may be more suitable for sticking on to the skin of the host than that of the *Chrysocharis* class, while the large body spines on the primary larvae of the latter group may be helpful in effecting eclosion from the egg, which may be more difficult of accomplishment in a fluid than in a gaseous medium. Or it may be that with the help of these spines the submerged endoparasite *casts off* the egg-shell, whereas in the case of the ectoparasite the egg may be held in position either by an adhesive or by the combined pressure of the skin of the pupa and the wall of the puparium, so that the larva is enabled to crawl or *wriggle out* of the shell. In this connection it is interesting to refer to the strong dorsal armature of the pea-moth pupa, as described by the present writer (1938), which enables the latter instar to free itself from its cocoon. Again, the presence of spiracles on the primary larvae of the ectoparasite and their absence from this stage in the endoparasite are undoubtedly correlated with habit of life. The degree of development of the tentorium would also seem to have some connection with the mode of existence, the stronger and larger structure, at any rate in the primary instar, possibly being better adapted to the more energetic life of the ectoparasite, and so on. Although some of these peculiarities of structure are almost certainly correlated with the life-habit, it is necessary to exercise a certain degree of caution when dealing with this difficult group of insects, because as Parker has shown in some of his examples, certain modifications which appear suited to the particular habitat are present in one species and absent in another, although the mode of existence of the two species may be very similar. We can, therefore, only point out that the presence or absence or degree of development of certain organs has some significance and some relation to the life-history of the species concerned, but we must await wider and fuller knowledge before we can become fully aware of the real import of the structural adaptations which we have just described.

Description of Technique employed in the Investigation.

A brief account of the methods used in the preparation of the immature stages of the Chalcid parasites of *P. ilicis* for microscopic examination, and certain other relevant technical data, may prove to be of somewhat general interest to the reader. The mountant employed in the majority of cases was Liquide de Faure. This excellent medium, which is composed of gum arabic 30 gms., distilled water 50 cc., chloral hydrate 50 gms., glycerine 20 cc., and cocain hydrochlorate 0·5 gms., has a low refractive index so that the finer structures of the larval head show up in it comparatively well. It has also the great advantage over other media in that the preliminary stages of bringing the material up through the alcohols, etc., associated with balsam mounts, is eliminated, and staining is generally unnecessary. Furthermore, the larva is usually fixed and mounted in a more natural position and the distortion which often accompanies other methods is reduced to a minimum. As a rule the living larva freshly dissected out of its host was placed directly, ventral side upwards, in a drop of the liquid on a slide. Then a coverslip, supported at the four corners by tiny pellets of plasticine, was placed over it and gentle pressure applied. If the head and cephalic skeleton were to face squarely upwards it was found that a certain amount of manipulation and observation of the mount under the binocular microscope was usually necessary. Sometimes it was more convenient to leave the larva in the required position on the slide until the medium had hardened somewhat, before placing the coverslip over it. Several hours to a day after preparation, the mounts cleared sufficiently for a satisfactory examination of the various structures to be made under high magnification. In addition to whole undistorted mounts of this type, which were used as controls to ensure that the true relation of each structure to the whole was maintained, both in the description and the illustration, further mounts were made in a similar manner and then pressure gradually applied to the coverslip in order to flatten the larva and press out the body contents. With such preparations certain details, especially of the skin, spiracles, and tracheae showed up better and all the parts could be more clearly discerned. A method which I have often found useful when dealing with Ichneumonid larvae, namely that of mounting the cast skin (which is usually to be found adhering to the faeces at one end of the cocoon) for the examination of the cephalic skeleton, was not found to be suitable for the Chalcids. The reason for this appears to be the mode of dehiscence of the larval skin ; in the Ichneumonids, the latter splits in the neck region and the head-capsule remains attached to it without suffering any material damage ; whereas in the Chalcids, or at any rate in those I have examined, the head-capsule itself splits and the cast skin is usually valueless for making a preparation suitable for illustrating the cephalic skeleton, although the mandibles, spiracles and skin structure can usually be determined. It can, however, once the adult has emerged and been determined, provide a very valuable clue to the identity of the larva.

Occasionally the skins and larvae were stained with carbol-fuschsin, a stain which I have found to be very suitable for parasite larvae in general. As a rule, however, with the method outlined, staining was seldom necessary. For showing up the tracheae and spiracles, glycerine jelly (previously warmed) was found to be an excellent medium, while the preservative which was generally employed for the immature stages of both host and parasites was Carnoy's fluid, or as it is sometimes called acetic alcohol (chloroform 3 parts, absolute alcohol 6 parts, and glacial acetic acid ½ part). This fluid is said to be one of the most penetrating and quickly acting fixatives known.

To determine the number of ecdyses in the larval stage of any particular parasite was often difficult, especially in the case of the endoparasitic species, but measurements of the head, mandibles, cephalic skeleton and spiracles, which showed a progressive increase in each instar, were useful guides. Often the larval skin of the previous stage was found adhering to the posterior end of the larva under examination and this was a great help in confirming previous conclusions.

As a rule Dipterous puparia, if one desires a good emergence of flies and parasites, are rather difficult to handle in the laboratory, chiefly because of their susceptibility to dry conditions. Gelatin capsules of the type used for administering various medicinal drugs, etc., have been employed successfully at Farnham House Laboratory for isolating and rearing to maturity larvae and pupae of Lepidoptera, etc., but the writer has found them to be less suitable for the puparia of Diptera, probably because of the drier atmosphere maintained within these tiny vials. With holly fly material miniature glass tubes fitted with corks, or plugged with cotton wool, have given far better results.

Summary.

1. In Canada, European holly (*Ilex aquifolium*) can only be grown successfully in the mild, humid climate of western British Columbia. The sales of cut holly for decorative purposes amount to several hundred thousand dollars annually, and the tree is also in good demand for ornamental planting in public parks and private estates.

2. The most serious pest of holly in this part of the world is the Agromyzid fly, *Phytomyza ilicis*, or the Holly Leaf-miner, which was accidentally introduced from Europe without its attendant natural enemies. The larvae of this insect produce large unsightly blotches on the leaves which greatly lower the value of the cut foliage. As a rule 75 to 80 per cent. of the leaves are attacked in this manner.

3. Since chemical forms of restraint offered little hope of success, it was decided that the biological method of control should be given a trial. Accordingly, the writer undertook a general survey of the fly and its parasites in England, the results of which are described in the preceding pages. An account of the biological control of *P. ilicis* will be published in a separate paper at a later date.

4. A general account of the systematics, synonymy, distribution, host relationship, and biology of the holly fly itself precedes the parasite section.

5. During the course of the investigation nine species of parasites, eight of which are Chalcids and one a Braconid, were obtained from holly fly material collected in the South of England. All of them were reared for the first time, so that nine new host records are thus established. The Braconid parasite on examination proved to be a new species. The biology of the most important of these parasites is dealt with, as well as the morphology of their early stages.

6. *Chrysocharis gemma* (EULOPHIDAE), which attacks the host larva, is the most important parasite of the Holly Leaf-miner. On an average it was responsible for the destruction of some 30 to 40 per cent. of the fly larvae, whilst the maximum parasitism attained by the species during the years 1937 to 1938 was 71 per cent.

7. *Chrysocharis syma*, like its congener, *C. gemma*, is also a primary parasite of *P. ilicis*. It comes third in order of importance in the parasite list. This species attacks the pupa and its average parasitism in 1938 was 3·1 per cent. with a range of 0 to 13·8 per cent. (It should be noted that the figures for parasitism are based on the number of mines and not on the number of puparia.)

8. *Pleurotropis amyntas* is a parasite which acts in both a primary and a secondary capacity—the species hyperparasitized being *Sphegigaster flavicornis* and *Chrysocharis syma*, etc. Although fairly generally distributed it was never found to be very common, its average parasitism in 1938 being only 0·4 per cent. and its range 0 to 1·5 per cent.

9. *Sphegigaster flavicornis*, which is primary in habit, attacks the pupa of its host. It comes second in order of importance as a parasite of *P. ilicis*, with an average parasitism in 1938 of 4·5 per cent. and a range of 0 to 16·6 per cent.

10. *Cyrtogaster vulgaris* is also a primary parasite of the pupa and like *Sphegigaster* belongs to the family PTEROMALIDAE. Its average parasitism was low, 0·4 per cent., and the range 0 to 6·7 per cent. A remarkable characteristic of this species is its ability to feign death when approached. Several females were kept in the Laboratory throughout the winter, and a new generation reared from them in the following spring.

11. *Opius ilicis* is the only Braconid parasite of the Holly Leaf-miner. It is a rare species, and only 0·3 per cent. of the mines were attacked by it.

12. The next section deals with certain morphological characteristics and their relation to a system of classification of Chalcid larvae, showing that the species here dealt with can be divided into two distinct systematic groups, which can further be distinguished by characters in the egg, prepupa and pupa.

13. A brief account of the technique employed in the preparation of Chalcid larvae for microscopic examination, together with notes on certain useful methods of handling material, brings the paper to a conclusion.

Acknowledgments.

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THE RESULTS OF SHIPMENTS OF THE PREDATORY ELATERID BEETLE *PYROPHORUS LUMINOSUS* FROM PUERTO RICO TO ENGLAND.

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At the request of Dr. W. R. Thompson, Superintendent, Farnham House Laboratory, The Imperial Institute of Entomology, England, arrangements were made in 1936 to collect and furnish to him larvae of the predacious Elaterid *Pyrophorus luminosus*, Illiger, indigenous to Puerto Rico. These beetles were for liberation in Mauritius to aid in the control of the white grub, *Phytalus smithi*, Arrow. Shipments were sent by steamer from Puerto Rico to New York and then to England for repacking and shipment to Mauritius. The Mauritius government appropriated the sum of 85 pounds sterling to defray the expense of collection, packing and shipment.

The larvae of *P. luminosus* are predacious in habit and feed upon a number of our insect pests. Wolcott[†] records *Pyrophorus* to be particularly effective against the white grub in Puerto Rico.

Since the introduction of the giant toad, *Bufo marinus*, in 1920 by the Puerto Rico Experiment Station[‡], the abundance of white grubs has been considerably reduced, particularly in the lowlands which are favourable to the toad. For this reason it was necessary to collect the predatory beetles in the mountainous regions where white grubs are to be found in greater abundance.

Arrangements for the collection of *P. luminosus* larvae were made with the "mayordomo," Juan Perez, of the Treasure Island Camps at Cidra, in the central mountainous section of the island. This location had been reported by Tucker and Wolcott[||] as a favourable section of the island for collection of *Pyrophorus*. The beetle larvae were paid for at the rate of 3 cents, U.S. currency, for large larvae and 2 cents. for small larvae. This charge included the supervision of collection, packing, and shipment to Mayaguez. On arrival at Mayaguez the larvae were checked as to mortality and species, and then were repacked for shipment to England.

Shipments from Cidra to Mayaguez were made in tin salve boxes. Each predatory beetle larva was placed in an individual box of $\frac{1}{4}$, $\frac{1}{2}$, or 1 ounce, dependent upon the size of the larva. The salve boxes were well filled with soil to prevent any excess movement of the larva within the box. The larval mortality averaged approximately 2 per cent. during this period in transit and was apparently due in the most part to injury of the larvae at the time of collection.

In the first shipment made to England various materials were used as packing media in order to determine the optimum survival of the larvae of the predator. All of the materials used were sterilized with live steam and moistened slightly at the time of packing. The following media were used : sifted soil, unsifted soil, sand, decayed coconut wood, equal parts of sand and soil mixed, and moss. By far the best results were obtained with the decayed wood of coconut, *Cocos nucifera.* Dr. Thompson in his first report recommended that less moisture be used. Later shipments were made without the addition of moisture, using only that which was present as a result of steam sterilization, and this practice gave excellent results.

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[*] Contribution from the Puerto Rico Experiment Station, United States Department of Agriculture, Mayaguez, Puerto Rico.

[†] Wolcott, G. N. "El Cucubano *Pyrophorus luminosus* Ill." Circ. No. 80, Insular Experiment Station, Puerto Rico, Oct. 1923.

[‡] May, D. W. "Surinam Toad." Annual Report Puerto Rico Agr. Exp. Station 1926, Mayaguez, Nov. 1927.

[||] Tucker, R. W. E. and Wolcott, G. M. "Parasite Introductions: Barbados and Puerto Rico." Proceedings of the Fifth Congress International Sugarcane Technologists. Queensland, Australia, 1935.

For experimental information in the laboratory a series of 36 *Pyrophorus* larvae collected at Cidra on 15th and 16th October were placed in seven different types of packing media, 6 specimens to each type. The media used had been steam-sterilized and moistened slightly. The larvae were placed in tin salve boxes of 1, $\frac{1}{2}$, $\frac{1}{4}$ ounce capacity according to the respective sizes of the larvae. Table I shows the mortalities observed in the different media from 19th October, 1936, to 26th January, 1937, when the experiment was discontinued.

TABLE I.

The Mortality of Pyrophorus luminosus *Larvae when packed in different Media.*

Type of medium	Number of larvae	Examination dates with number dead							Total number dead
		19 Oct.	26 Oct.	2 Nov.	14 Nov.	28 Nov.	15 Dec.	26 Jan.	
Sifted soil ...	6	0	2	0	2	0	1	1	6
Unsifted soil...	6	0	2	0	2	0	1	1	6
Sand ...	6	0	0	0	0	0	1	1	2
Decayed wood	6	0	0	0	0	1	0	0	1
Soil and sand	6	0	0	0	0	1	0	0	1
Moss	6	0	0	0	1	0	0	2	3

A number of the larvae moulted once during the experiment and several larvae moulted twice. No additional moisture or food was added throughout the experiment. The two soil media became hard and ball-like in structure, and I believe that this physical character of the soil played an important part in the resulting mortality. All the other media retained their loose structure.

A total of 11,281 larvae of *P. luminosus* was sent from Puerto Rico to England from 22nd October, 1936, to 28th January, 1937. W. F. Jepson, Government Entomologist of Mauritius, who was in England when the larvae arrived, commented as follows on their condition : " The survival of the larvae during the voyage to England has been very good throughout. In the first few shipments, some mortality resulted through exposure to low temperatures at this end, but this was overcome in later shipments. In the last shipment, out of 1,896 larvae shipped, 1,650 were available for shipment to Mauritius. Out of the total 11,281 sent from Puerto Rico, 8,127 were despatched to Mauritius. It is as well that the work has been concluded at this season, for the first pupae were found in the final shipment."

This represents a 72·04 per cent. survival for all shipments and 87·02 per cent. for the final shipment of 1,896 *P. luminosus* larvae made on 28th January, 1937, from Puerto Rico to England.

PROBLEMS CONCERNING THE EFFICIENCY OF OILS AS MOSQUITO LARVICIDES.—II. THE SPREADING POWER OF OILS AND METHODS OF INCREASING IT.

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Introduction.

A previous communication (Murray, 1938) has dealt with the stability of films of oil which initially covered the whole of an area of water surface ; the problem now under attention is that of covering the maximum area of water in the first place.

Spreading is dependent on surface tension. It occurs if the sum of the air-oil surface tension and the water-oil interfacial tension is less than the air-water surface tension. Put in the form of a mathematical relation, where σ represents the numerical value of the tension in dynes/cm. this reads :—

$$\sigma \text{ air/oil} + \sigma \text{ water/oil} < \sigma \text{ air/water}^{*}$$

The right-hand term is constant for clean water, and there is thus a sharp transference from no spread to spread when the interfacial tension of the oil is lowered. There is no possibility of partial spread. But when the water surface is " dirty," that is to say, contains molecules of other substances, the right-hand term is lowered and is no longer constant, but tends to be further lowered as these molecules are pressed closer together by the advancing oil. Partial spreads may thus occur ; the extent of spread is determined on the one hand by margin of dynes/cm. by which the air-water tension can be lowered from the pure water figure before equalling the sum of the two left-hand terms, and on the other hand by the resistance of the contaminating molecules to compression or displacement from the surface. While the latter will remain a local varying factor, the former is a quantitative measure capable of determination with considerable accuracy. Through the remainder of this report it will be referred to as the " spreading pressure."

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*This relationship is often deduced from the assumption that surface tension is a force tangential to the surface tending to reduce the surface area to a minimum. This concept of surface tension, though still found in many text-books, is incorrect. Exactly the same relationship is arrived at by Harkins and Feldman (1922) who define as the condition for spreading that the work of adhesion for the interface of the liquids must exceed the work of cohesion of the liquid being applied to the surface. As the terms have the units ergs/sq. cm. instead of dynes/cm. the numerical magnitude of the inequality is called by Harkins the "spreading coefficient" and not "spreading pressure."

An Adam-Langmuir trough was used for the measurement of this spreading pressure (*vide* Adam, " The Physics and Chemistry of Surfaces "). The water surface in front of the float was covered with a unimolecular film of some material, which was then compressed to any desired extent by moving up the waxed glass barrier. (The choice of a suitable substance for this film, which is important, will be considered on pages 214 to 215). The spot of light reflected from the mirror was brought back to the zero position by turning the torsion head, and the compression of the film measured in dynes/cm. by multiplying the torsion head reading by a factor determined during the calibration of the instrument. A drop (about 0·02 cc.) of oil was then delivered from a pipette on to the unimolecular film. If an immediate spread occurred, the glass barrier was moved up further and another drop added at the new compression, until the point was reached where the oil made no immediate spread. If no spread occurred in the first experiment, the barrier was moved away from the float before adding the second drop.

With this apparatus measurements could be made rapidly and with very small amounts of material. It was desirable not to allow oil to touch the float, the waxed barriers or the waxed sides of the trough. For this purpose the maximum number of drops on the surface at any one time should be about eight. The drops were removed in the following way : a glass barrier was placed between the float and the nearest oil drop, and then moved so as to compress the film further ; when the drops were squeezed up they were removed with a spoon. This method was generally successful if the spreading pressure of the oil did not exceed the collapsing pressure of the unimolecular film. If it exceeded this value of course no amount of compression would shut the oil back into a lens, and oil ran on to the barriers and sides, dissolving the wax. Even so, all that was usually necessary was fresh waxed barriers, though sometimes the whole apparatus would require re-waxing.

To commence this study a survey was made of the spreading pressures of a large number of samples of oil, all products or by-products of normal refinery processes. Some white oils and lamp kerosenes were found to be non-spreading. Among oils which spread, very diverse values ranging from 8 to 20 dynes/cm. were obtained. Values between 0 and 8 dynes/cm. were not found. An oil marketed in India as a special anti-malarial oil had an S.P. of 25 dynes/cm., but it was assumed that it contained some additional product not necessarily of petroleum origin.

The most comprehensive account of spreading pressures in the existing literature is that by Harkins and Feldman (1922) quoted in the footnote on page 211. Harkins (1928) retabulates the results in a more convenient form. While lower paraffins up to octane spread (not every isomer has been studied), higher ones are non-spreading. It is very difficult to obtain pure aromatic hydrocarbons of a boiling range comparable to the higher paraffins, but all investigated aromatics range between 6 and 10 dynes/cm. No saturated hydrocarbon exceeded this figure. Two unsaturated hydrocarbons are quoted with very high spreading pressures, 18 and 22 dynes/cm., but the present writer thinks these should be taken with reserve, since this class is readily reactive under the influence of light and yields oxygen-containing compounds of high spreading pressure. The two unsaturated hydrocarbons used in this work, styrene and di-isobutylene, when freshly distilled did not exceed saturated hydrocarbons in their spreading power (*cf.* also Johansen, 1924).

There thus appeared a *prima facie* case for supposing that oils with a spreading pressure of greater than about 12 dynes/cm. owe this property to non-hydrocarbon constituents, which only make up a very small percentage of the whole. A closer scrutiny of the preliminary results was then made and the following points were noticed. Among products of the kerosene boiling range (say 150°C.–270°C.) high spreading pressure was associated either with high unsaturated content, or with long storage of the sample, particularly if storage had been in glass bottles exposed to light. New samples purporting to be similar to the stored samples had normal low figures, supporting the idea that storage was responsible for the change. Exposure of the new samples to light, even diffuse daylight, proved that this was the case ; further, the smaller the sample and the shallower the oil layer, the sooner was an increase of spreading pressure observable, until for a sample of 0·5 cc. spread in a watch-glass an increase was measurable after an hour. Similar observations were made by Johansen (1924).

It was also shown that distillation of the stored samples gave distillates of spreading pressure similar to that of the new samples ; in other words the bulk of the oil can be recovered unchanged, only a small proportion undergoes alteration.

Oils of the gas oil range (say 230°C.–370°C.) were less regular in their properties, some showing high spreading pressure when fresh, but work to be described showed that the spreading constituents were easily removable and that nearly all of the oil was recoverable with low or zero spreading pressure. The conclusion that oils owe their spreading properties to constituents present only in very small amounts and never mentioned in the usual system of specifications is one that will be continually emphasized in this paper.

It would be the ultimate object of work of this kind to discover the constitution of these substances, such small quantities of which produce such great changes in the spreading properties, but no attempt has yet been made to face problems which oil chemists agree are in the present state of our knowledge insoluble. On the other hand important progress in concentrating the active products has been made by bringing a few well-known physico-chemical principles to bear on the problem.

In contrast to the analytic method is the method of synthesis of an actively spreading mixture. For this purpose a standard oil of low spreading pressure was chosen and the effect of dissolving different substances in it studied. The substances chosen were, firstly, comparatively simple representatives of the chief classes of organic compounds, with a view to determining what chemical groupings are active. More complex substances were tried if their use seemed of special interest. For example, in view of the discovery that light causes the formation of active substances, polymerised hydrocarbons and derivatives in which combined oxidation and polymerisation had occurred were tried, since the substances arising from the action of light would very likely be of this type.

Synthesis of a spreading mixture without the addition of any other substances was also studied. The action of light is the only method so far found of bringing about the desired chemical reaction.

The experimental section of this work therefore falls under the following heads :—

1. Problems of technique, that is of adapting the Adam-Langmuir surface pressure apparatus for the purpose of measuring the spreading pressure of oils. Several other interesting points bearing indirectly on this are treated here.

2. Methods of increasing the spreading pressure of oils, (*a*) by bringing about changes in the oil itself, and (*b*) by adding other substances to the oil.

3. Methods of concentrating the actively spreading substances which are found in commercial oils.

Some Comments on the Use of the Adam-Langmuir Surface Pressure Apparatus for Measurement of the Spreading Power of Oils.

A complete description of this apparatus is given by Adam (" The Physics and Chemistry of Surfaces," 2nd Edition, 1938, pp. 26–33). The method of using the apparatus for this type of work has been explained at the commencement of this paper. There remains here a few points requiring more detailed discussion. Although the apparatus measures pressures it would not be practicable to put oil directly on the cleaned water surface. This would inevitably result in oil flowing all over the waxed parts of the apparatus, but in addition any readings made would be uninterpretable and probably not reproducible, since once the polar materials in the oil had had opportunity to escape into the interface complications could arise. The use of a " buffering " film consisting of an oriented monolayer is indispensable.

The next necessity is to enquire whether the results obtained are independent of the nature of the buffering film. On theoretical grounds they are obviously not, but must depend on the ease of compression of the monofilm. Adam (*loc. cit.*) has summarised the results of himself and co-workers on the construction of " force-area " curves showing the relation of the pressure in dynes/cm. on the float to the area of surface occupied by unit number of molecules. Upon the slope of the force-area curve depends to some extent the estimate of spreading pressure made by this method.

Consider what occurs when a drop of oil is added to the surface on which the pressure of the monofilm F falls short of the spreading pressure by a small amount Δ F. The oil spreads and causes a corresponding small diminution in area of the monofilm of Δ A, stopping when the rise of pressure Δ F has brought it to the spreading pressure. Then $\Delta A = \Delta F \div \frac{dF}{dA}$. Now it is Δ A and not Δ F which the eye observes, and if the observer keeps the same criterion of spreading his estimates of F the spreading pressure will not be the same for substances of different $\frac{dF}{dA}$. If $\frac{dF}{dA}$ is large and thus Δ A small he will underestimate F ; if $\frac{dF}{dA}$ is small, allowing a very large Δ A, he will form too high an estimate of the spreading power. Even for the same substance $\frac{dF}{dA}$ does not remain constant at all compressions but it was estimated that unless it changed very greatly the error was not enough to affect this work adversely.

It was found that oleic acid made a suitable buffering film for all pressures up to about 25 dynes/cm., above which its liability to collapse made it inconvenient. It was in making readings above this pressure that the difficulties now under discussion arose. Cholesterol withstands pressure of 35 dynes/cm., but the film is of the condensed type (*vide* Adam, p. 49) and $\frac{dF}{dA}$ is very high. Once a pressure is registered at all, the smallest reduction in area is accompanied by great rise in pressure the latter trebling itself in an area reduction of one or two per cent. On the other hand, certain petroleum sulphonates (see page 225) which also withstand 35 dynes/cm. pressure form such expanded films that the area has to be reduced to half in order to double the pressure. Between these rather extreme cases the possible divergence in the reading of the spreading pressure is large ; the spread against a cholesterol film at 28 dynes/cm. compression is actually not so large as that against a film of the sulphonate at 34 dynes/cm.

Reference has been made to the upper limit of pressure measurements being fixed by the collapse of the film at high pressure. Adam has referred to this collapse of films in the earliest of his series of papers (1921), but there are not many later references. The more important facts can be briefly put as follows. Some substances are capable of being spread not only from solution in light spirit but also directly from the liquid or even solid state. When added in excess, they spread until an equilibrium pressure is reached which is a constant for any given temperature and ionic concentration in the water. If the area is increased, more spreads from the reserve, if diminished, molecules presumably return to the excess from the film. Castor oil was an excellent example of such a substance ; a pressure of 15·5 dynes/cm. was registered when the barrier was 30 cm. from the float, which only increased to 16·6 dynes/cm. when the barrier was moved up to 2 cm. from the float. Behaviour of this kind obviously imposes a definite upper limit to measurements, and in addition since $\frac{dF}{dA}$ is tending to zero no reliable readings can be taken near this limit. The sulphonic derivative referred to, although not actually spread from the solid, gave a similar definite limit, though in this case it was the high one of 40 dynes/cm. Several other products obtained during the analytical part of this work (page 234) also behaved like this.

On the other hand there are substances which behave in an almost exactly opposite way. With these substances the monofilm is either solid or becomes solid at a certain compression. The difference between a solid and a liquid film is easily demonstrated by scattering a light powder on the surface and then directing a fine jet of air at it ; on a liquid film the particles move about just as on water but on a solid film they remain motionless. The solid film resists compression, and when the barrier is moved up to decrease the area there is a big rise in pressure. It is not in equilibrium, however, and the film may undergo collapse at any moment, that is, a portion of it may be expelled from the surface to relieve the pressure. It is possible, though not very convenient, to measure the spreading pressure of oils under such conditions.

Information was then sought on the following point. The spreading pressure of a solution of a substance in oil rises with increasing concentration of the substance until a " saturation " pressure is reached. Is this pressure equal to the maximum pressure exerted by the substance when it forms a monolayer ? If so, substances could be tested very rapidly for their value as spread-aiders, by monolayer experiments not involving oil solutions. On this point the literature was unhelpful. N. K. Adam in private communication gave the opinion that a substance might be expected to give much the same properties to an oil-water interface as to an air-water one, if its concentration were sufficient to saturate the interface, unless there was a great attraction between the molecules of the substance and of the oil solvent, in which case the saturation pressure for the oil-water interface might be lowered. (The results in the section beginning page 227 bear this out.)

Owing to the fact that many substances which give an increased spreading pressure to oil are too soluble to admit of film measurements, while on the other hand there are substances which withstand pressures much higher than they are really in equilibrium with, there is only a limited group of substances yielding compression curve data that can be used in this connection. Within this limited field, however, there is practical value in the data ; for instance, in the work on separation and concentration of the active constituents already in oils (pages 229 onwards) the monofilm method was repeatedly used as a rapid test for the presence or absence of the substances in any particular fraction, and in every case the longer method of making oil solutions confirmed its validity.

Except where otherwise stated, the buffering film throughout the following experiments consisted of oleic acid, but the sample which was used had undergone slight autoxidation, which made the film rather more stable at higher compressions.

The water in the trough was kept at neutrality by the addition of a little phosphate buffer (*p*H 7), about 50 cc. M/5 phosphate in the whole volume of about 1,650 cc. Distilled water was used to prevent precipitation of calcium salts.

Methods of Raising the Spreading Pressure of an Oil by Physical or Chemical Treatment of the Oil.

The original observations suggest that a change in the spreading pressure can arise spontaneously in the oil, that is, without any chemical treatment. The first investigation was therefore directed to the study of the action of heat and light.

An oil of mixed composition, that is, containing both aromatic and aliphatic hydrocarbons, was taken. It was a sample of the normal intake oil of an Edeleanu plant at Balikpapan, boiling range 137°–290°C., 60 per cent. insoluble in liquid SO_2. It had a spreading pressure of 10·8 dynes/cm. ; 20 cc. was heated for an hour under a reflux condenser with ground-glass fittings so that the vapour did not come into contact with any rubber. The spreading pressure was measured again after the oil had cooled, but no change was observable within experimental error. Two samples each of 5 cc. were subjected to one hour's irradiation from a mercury vapour lamp, the oils being spread out in flat circular dishes, one 5 cm. diameter and one 9·5 cm. diameter. The spreading pressure of the former was found to be slightly raised, namely to 13 dynes/cm., but that of the latter was raised to 18·5 dynes/cm. Evidently irradiation of a thin layer leads to chemical changes which occur only to a less extent when the layer irradiated is thicker, and do not occur on heating the oil. It was considered desirable to try the effect of heat on a thin layer, which was achieved by use of a small flask with two flat parallel circular faces heated on a sand-bath. After a quarter of an hour's heating during which vapour condensed and ran back from the upper face, the spreading pressure was found to be unaffected.

Since in general, olefines are the most reactive group of hydrocarbons, and in particular it had already been observed that pressure distillate readily acquired active spreading properties, the next experiments were directed to investigating whether the photo-chemical effect was proportional to the content of olefines in the oil. Gas oil was chosen for these experiments since through the courtesy of the companies financing this work a number of grades were available. Four " straight " gas oils from different parts of the world and one " cracked " gas oil were compared. The cracked gas oil had a McIlhiney bromine value of 23 and an aniline point of 54°C. ; the straight oils had all McIlhiney values of less than 1·0, but the aniline points varied, two (Burmah and Iranian) being 72°C., but the other two (Roumanian and Venezuelan) being only 57°C., 5 cc. of each oil was placed in Petri dishes of 4 inches diameter. The dishes were specially made and the bottoms were optically flat ; it is, however, not possible to determine the thickness of the layer which is being irradiated since the amount in the meniscus is a great deal too large to be neglected.

TABLE I.

Change of Spreading Pressure of Gas Oils on Irradiation with Light from a Mercury Vapour Lamp.

Description of oil	Initial S.P. (Dynes/cm.)	Final S.P. (Dynes/cm.)
Straight gas oils—		
Burmah	13·5	23·5
Iranian	10·5	34·0
Venezuelan	18·5	30·0
Roumanian	16·0	30·0
Cracked gas oil (Iranian) ...	25·0	36·0

Each dish of oil received one hour's irradiation from the mercury vapour lamp, the distance from the lamp being the same in every case.

The changes in spreading pressure are summarised in Table I.

A very striking effect was thus caused in all the oils. The straight oils differed as much among themselves as from the cracked oil, which did not appear to undergo a greater change. A handicap in this experiment was the great irregularity of the initial spreading pressures. A more accurate experiment became possible when it was shown that actively spreading material already present in the oil could be readily extracted with certain solvents. The oils in the following experiment were the same Roumanian gas oil and cracked gas oil as the above, after extraction with methyl alcohol had brought down the spreading pressure of each to 11 dynes/cm. A small change in the hydrocarbon make-up of the oil is made in this process, since the small amount of aromatic hydrocarbons presumably goes into the methyl alcohol also. A series of samples of 0·25 cc. oil was placed in a row of similar watch-glasses which were then exposed to a similar illumination, the contents of each watch-glass being used for only one measurement. The glasses were four hours in diffuse daylight, during which time (Table II) very little change occurred in either ; the remaining ones were then transferred to direct sunlight and change was rapid (Table III). The difference between the two kinds of oil, straight and cracked, is almost negligible.

TABLE II.

Change of Spreading Pressure of straight and cracked Gas Oils on Exposure to diffuse Daylight.

	½ hour (Dynes/cm.)	1 hour (Dynes/cm.)	1½ hours (Dynes/cm.)	2½ hours (Dynes/cm.)	4 hours (Dynes/cm.)
Straight (Roumanian) ...	11·5	12·1	12·6	12·6	12·6
Cracked	11·6	12·1	12·5	12·6	12·6

TABLE III.

Change of Spreading Pressure of straight and cracked Gas Oils on Exposure to direct Sunlight.

	½ hour	1 hour	2 hours
Straight (Roumanian) ...	20·8	25·8	29·0
Cracked	21·0	26·0	27·5

There is therefore no evidence that olefinic hydrocarbons are more photo-reactive than any other kind, a conclusion which it must be confessed was not what was anticipated, but which is in agreement with the results of Johansen (1924).

Certain information can be obtained from " dilution curves " of the irradiated oil. If it be supposed that by irradiation a small quantity of the oil is transformed into a new compound, the bulk of the oil being unchanged, then by mixing the irradiated oil with the original unirradiated oil the active substance is diluted. By a series of mixtures in different proportions a curve may be drawn in which the ordinate is the spreading pressure, the abscissa the concentration of the active substance, although the scale of the abscissa must be quite arbitrary. When such curves are drawn it is found that they have a common shape which is not linear ; they are all convex upwards, and already by a mixture of equal proportions of irradiated and untreated oil the maximum spreading pressure is almost reached. The following table enables one to construct such curves.

TABLE IV.

"Dilution Curves" of irradiated Gas Oils.

Burmah			Iranian		
Parts unirr.	Parts irrad.	S.P. (Dynes/cm.)	Parts unirr.	Parts irrad.	S.P. (Dynes/cm.)
4	0	13·0	4	0	11·0
3	1	19·7	3	1	23·0
2	2	21·0	2	2	25·6
1	3	22·8	1	3	27·1
0	4	23·9	0	4	28·0

Many others of the same shape could be reproduced.

Evidently the substance responsible for the change is active in very small concentration, and above a certain concentration, which is still comparatively small, the oil-water interface becomes saturated with the substance and further increase in concentration is more or less ineffective. One might suppose from this that however long the oil was irradiated the spreading pressure would not rise further than this "saturation" value, which can be deduced by extending the curve. But this does not turn out to be the case. When samples of the same gas oil were irradiated for different periods, the spreading pressures were all different, showing a steady increase with time of irradiation. Each gave a smooth dilution curve but each with a different "saturation" level. From this may be drawn the conclusion that there is not one single product formed, but a series of several, probably formed progressively from one another. In any irradiated sample there is present a mixture of these in various proportions.

A comparison of Tables I and III shows that the use of a mercury vapour lamp is unnecessary, since sunlight even through a glass window is quite effective. The light of an ordinary electric filament lamp proved ineffective for gas oils and kerosene extract, but produced a slow rise of spreading pressure in Malariol. Although the dark colour of this oil would lead to more absorption of irradiation, the change is more probably attributable to its content of unsaturateds (McIlhiney bromine number 12·5), since another dark oil was unaffected. Olefinic oils are the only ones which show an increase of spreading pressure after storage in the dark. In other cases we must assume that rays from the ultra-violet part of the spectrum are the agency promoting reaction.

The fact that the reaction proceeds equally in both saturated and unsaturated hydrocarbons appears to rule out polymerisation. It is probably a case of oxidation, though the nature of the product formed is not obvious. Attempted oxidation of oils by chemical reagents has failed to bring about any similar change. One of the objects of the next section of this work, in which various types of organic compound were dissolved in oil as possible spread-aiders, was to get a clue to the structure of this natural substance.

Changes produced in the Spreading Pressure of an Oil by dissolving certain substances in it.

The practice of dissolving substances in oil to improve it for anti-mosquito work is almost as old as the use of oil itself. Sometimes the added substance has been intended to improve toxicity, more often to improve spread. The object of the part of the work now to be described was to measure the effect on the spreading pressure produced by dissolving certain substances in oil. Of particular interest was the quantitative comparison between such effects and those just considered. Their magnitude as compared with the wide range of values found for untreated oils was also of obvious importance.

The types of substance used to add to the oil have already been mentioned (page 213). They are grouped here under the following paragraph headings :—

1. Carboxylic acids and esters.
2. Alcohols and phenols.
3. Other organic compounds of known composition.
4. Polymerised hydrocarbons.
5. Substances derived from hydrocarbons by combined oxidation and polymerisation.
6. Sulphonated derivatives of hydrocarbons.

1. *Carboxylic acids and esters.*

In this group fall fatty acids and vegetable oils, which have been recommended from time to time. Naphthenic acids also belong to this category, and the question as to how far the spreading pressure of untreated oils is influenced by the content of these naturally occurring constituents can be answered.

Although fatty acids have been ruled out as useful spread-aiders as a result of experiments described in the previous communication, they were investigated to determine the effect of the simple –COOH group on spreading pressure. The first results recorded below were obtained with myristic acid. This saturated straight-chain acid was chosen because being a crystalline solid it is obtainable in a purer state than most of the others. The results gave a clear indication that this type of substance does not have a very great effect on spreading pressure (Table V).

TABLE V.

Spreading Pressure of Solutions of Myristic Acid in medium Kerosene Extract.

Percent. myristic acid	—	0·5	1·0	1·5	2·0
Spreading press. (dynes/cm.) ...	9·0	10·4	11·5	12·1	12·5

The oil in which the myristic acid was dissolved was a mainly aromatic oil and had been stored in a tin, hence its own spreading pressure was small. The weak action of myristic acid is made clear by contrasting this result with Table I.

Oleic acid being a liquid is less easily purified, and being unsaturated is more chemically reactive. It was not therefore surprising that different samples of this substance gave different increments of spreading pressure to oil. The samples referred to in Table VI had the following origins :—Samples A, technical oleic acid,

TABLE VI.

Spreading Pressures of Solutions of Oleic Acid in medium Kerosene Extract.

	Percent. oleic acid						
	0·5	1·0	1·5	2·0	2·5	3·0	4·0
Spreading pressure—							
Sample A	13·0	13·7	14·5	—	15·3	—	15·9
,, (dupl.)	13·2	13·8	—	14·5	—	—	—
,, B	16·3	17·8	—	19·3	—	—	—
,, C	16·1	17·6	18·4	18·9	—	19·1	—
,, D	20·6	21·9	22·8	23·9	—	—	—

but the sample drawn by pipette from the interior of the liquid which was in a brown bottle ; sample B, a small sample prepared by hydrolysis from olive oil ; samples C and D, a small sample left exposed to air and light at the bottom of a glass tube, C was prepared from this by shaking the solution of this in petrol ether with fullers' earth, D being the sample used directly.

A fair conclusion would seem to be that the action of an unsaturated acid, if pure, cannot greatly exceed that of a saturated acid, and is not of a great order in comparison with substances which are often present already in the initial oil. The greater reactivity of unsaturated acids, however, gives reason to suppose that they would frequently be contaminated with substances active in spread-promoting properties.

It was not surprising to find next that naphthenic acids were distinctly poor promoters of spread. The sample used was one supplied by the Shell Co. and neutral oil was removed from it by shaking the alkaline solution with petrol ether with subsequent reacidification of the clear aqueous layer. Table VII shows that the acid so produced was itself of poor activity but that once again it proved possible to obtain an active agent from it by no other means than exposure to light and air.

TABLE VII.

Spreading Pressures of Solutions of Naphthenic Acid in medium Kerosene Extract.

Sample A. Naphthenic acid freed from neutral oil as described above. Sample B. A thin layer of A in the bottom of a small beaker was protected from dust but exposed to air and light for several weeks, then used without further treatment.

Percent. naphthenic acid	—	0·25	0·5	1·0	2·0	
Spreading press. : Sample A	8·9	10·5	11·2	12·1	13·4	dy/cm.
,, B	8·9	12·1	13·9	17·3	20·2	,,

Passing to esters of carboxylic acids, olive oil was tried as a contrast to oleic acid. Table VIII shows that it is about as active as the purer preparations of oleic acid.

TABLE VIII.

Spreading Pressures of Solutions of Olive Oil in medium Kerosene Extract.

Percent. olive oil	—	0·25	0·5	1·0	2·0
Spreading pressure	9·5	12·1	12·8	13·4	14·3

Among vegetable oils that have been recommended for use as spread-aiders castor oil immediately comes to mind from the valuable work of Leak (1921). The fatty acid in castor oil, ricinoleic acid, differs from the fatty acids already used in containing additionally a hydroxyl group, thus rendering it even more reactive. Both castor oil and ricinoleic acid have been tried in the course of this work. The castor oil used was a good medicinal brand labelled " tasteless cold drawn castor oil." It was shown in several experiments, however, that 15·5 or 16 dynes/cm. was the maximum figure to which it could raise the pressure of the medium kerosene extract which had formed the standard oil throughout the series. The " technical " ricinoleic acid used was more active than the corresponding grade of oleic acid, but was about equal to the samples B and C of Table VI : 1 per cent. solution gave an S.P. of 18·2 dynes/cm. Ricinoleic acid was able to produce its effect in lower concentrations than oleic acid. The data did not suggest, however, that the exposed and activated oleic acid could owe its effect to the formation of a hydroxy derivative.

The same conclusion was reached from a brief experiment in which oleic acid was oxidised by alkaline permanganate in hot aqueous solution, conditions in which the major product is said to be dihydroxy-stearic acid. The white solid produced did not seem very soluble in oil and the solution so formed was less active in spreading properties than the oleic acid itself.

Another group of carboxylic acids which should not be overlooked is the bile acids. These are hydroxy-carboxylic acids built up on a structure of saturated carbon rings. The alkali salts of these acids are well known for their power of forming solutions of very low surface tension. These substances, together with the related sterols, will, however, be considered in paragraph 3.

2. *Alcohols and Phenols.*

Of all the substances used for adding to oils for mosquito control work, crude cresol has perhaps been the most popular and widely employed. In order to appraise its true value, however, it was replaced in this study by crystalline phenol, which was dissolved in the same medium kerosene extract of moderately low spreading power (S.P. 9 dynes/cm.). The results obtained were of the very greatest interest and of far-reaching importance, for they have a bearing on the whole question of the use of water-soluble spread-aiders.

Among all the types of oil so far discussed, whether their spreading powers are high or low, it has always proved that if drops of two oils are placed on the same contaminated surface, the one of greater spreading pressure will spread at the expense of the other, regardless of which is put on first. If the more powerfully spreading is added first, the other will fail to spread; if the less powerfully spreading is on first, then its drops will be forced to contract when the other is added to the clear area of the surface. Further, if several drops of the same oil are placed separately on the same contaminated surface, the later ones, although spreading more slowly owing to the increased pressure of the compressed contaminating film, will force the first ones to contract until all are of equal size. The solution of phenol in oil does not conform to either of these generalisations. A 5 per cent. solution was found to spread at 23 dynes/cm., a pressure high enough to enable it to force back advancing drops of many oils, but after a period of only a minute the phenolic drops were observed to be contracting and the other oil drops to be expanding again. Experiments on the Adam-Langmuir trough showed that while drops certainly showed an immediate spread at 23 dynes/cm., they contracted back to lenses in a few seconds, and after a minute the pressure could be released down to about 18 dynes/cm. before they once more opened out. If at this point a new drop was added, it spread vigorously and at once closed the others up. These observations admit of only one explanation. From the moment of contact with water, the spreading pressure begins to fall. Clearly the phenol, which is water-soluble, is escaping from the oil solution into the water.

Observations with other water-soluble alcohols confirmed this conclusion. With a solution of caprylic alcohol in oil drops were found to spread out momentarily and then to contract back. With the more soluble amyl alcohol the same occurred and it was further observed that at lower pressures the drop broke up with explosive violence, the broken patches then showing, however, no further tendency to spread. Finally with ordinary ethyl alcohol mixed with the oil it was found that at pressures up to 25 dynes/cm. the oil was thrown violently about the surface but was then left in tiny lenses; there was therefore no increase in spread. A momentary small spread occurred against pressures exceeding 30 dynes/cm.

One is forced to the conclusion that the theory on which the widespread use of cresol is based is fallacious. It is proved that when it is used in conjunction with clean oils it serves no useful purpose, though there might be types of oil to which the addition of cresol could be useful. For instance, there are other exceptions to the general rule outlined above that spreading oil is forced back into lenses again by oil of greater spreading pressure. With certain oils which have accumulated large amounts of active polar substances, *e.g.* distillation residues, the spreading is irreversible. No amount of increase of resisting pressure can force back the oil into a lens. In these cases one can assume that the active polar materials have firmly anchored themselves to the water interface so that only very great force can dislodge them. If cresol gave to these oils an increase of spread it would be permanent. On the other hand, they nearly always have such a high spreading pressure of their own that they would need no spread-aider.

Two other straight-chain alcohols, dodecyl and hexadecyl (cetyl), gave a maximum spreading pressure of only about 16 dynes/cm. This is the same order as the spreading pressure of the straight-chain fatty acids, and the two groups also both show the same tendency to leave the oil and enter the air-water interface, forcing the oil back.

Experiments with cholesterol, also a saturated alcohol, will be included with bile acids in paragraph 3.

3. *Other organic compounds of known composition.*

After the results with phenol, it was expected and confirmed that the simpler representatives of other groups such as amines, aldehydes, etc., are also rendered of no value as spread-aiders through their water-solubility. This paragraph will therefore be confined to a few miscellaneous compounds which for one reason or another were considered likely to be interesting, though in most cases it was expected that the interest would be only from the academic angle.

Benzoyl peroxide.—There have been suggestions (N. K. Adam, private correspondence with writer ; *cf.* also Brooks, ref. p. 224) that the product of photochemical oxidation of hydrocarbons has the structure of an organic peroxide. The effect of a simple representative of this class of compounds was therefore tried. The objection against simple compounds lodged previously does not apply here since benzoyl peroxide is insoluble in water. It was a matter of some surprise to discover that when this substance was dissolved in kerosene extract hardly any rise in the spreading pressure occurred. The maximum figure attained in saturated solution was only 13 dynes/cm.

Camphor.—Camphor is a derivative of the terpenes, a group of cyclic hydrocarbons, and it contains an oxygen atom in a ketonic linkage. It is readily soluble in oil. The upper limit of spreading pressure reached by dissolving it in medium kerosene extract was 16·3 dynes/cm., a value only reached, however, at a concentration of nearly 10 per cent.

Sterols and bile acids.—In the discussion on page 215 it was pointed out that substances dissolved in oil may give spreading pressures up to but not exceeding the limiting pressure which they can give as monolayers in equilibrium with excess. It was also disclosed that cholesterol withstood a very high pressure. While, owing to the condensed nature of the film, cholesterol undoubtedly withstands pressures greater than the equilibrium, a state near to equilibrium exists so long as a drop of solution of the substance in light spirit or benzene is floating on the film, and the pressure under these conditions is 32 dynes/cm. Now the only polar group in cholesterol is a single alcoholic –OH (there is also one double bond). Straight-chain alcohols have already been shown to give pressures not exceeding about 16 dynes/cm. It was therefore important to discover whether the spreading pressure of a solution of cholesterol in oil was of the order of 32 or 16 dynes/cm. The results are shown in Table IX.

It thus proves that cholesterol gives to oil a spreading pressure much greater than that given by straight-chain alcohols. Experiments were then extended to

TABLE IX.

Spreading Pressures of Solutions of Cholesterol in medium Kerosene Extract.

Percent. cholesterol	1·0	2·0	3·0	4·0
Spreading pressure	18·9	24·5	27·2	28·2

the bile acids, which have the same carbon skeleton as cholesterol (that is, a phenanthrene nucleus with a further 5-membered ring attached in the 7, 8 position). The bile acids differ from cholesterol in having four polar groups, three –OH groups in the nucleus instead of one, while the side-chain, non-polar in cholesterol, is terminated by a –COOH group. With both substances the measurements are very subject to the difficulties described earlier, owing to the high pressures exerted and the strong tendency of the material to leave the oil and enter the air-water interface (*cf.* action of oleic acid and petroleum sulphonate " A ", as described on pp. 23–24 of the previous communication), but there is little doubt that the figure for bile acid dissolved in the same oil is also 28 or 29 dynes/cm., a figure very near to that given by cholesterol, and considerably in excess of that given by any straight-chain fatty acid.

The action of these substances has not at present been followed up, but it is clear that a point of considerable theoretical interest is raised. It leads to the suggestion that the spreading properties are dependent not so much on the nature of the polar group as on the structure of the rest of the molecule, which is non-polar. A polar group is essential, for hydrocarbons are without surface activity, but its nature is perhaps not of importance ; a simple hydroxyl or carboxyl group may be the means of giving a high spreading pressure, provided that it is attached to the right sort of hydrocarbon framework. This could explain why there appear to be several different groups of actively spreading derivatives of the oil hydrocarbons themselves, substances produced by oxidation, sulphonation, etc., all showing activity of the same order.

It is now desirable, however, to pass on to the other groups of substances, which are not of accurately defined composition, but which present an expectation of interest.

4. *Polymerised hydrocarbons.*

The chemical reaction brought about by the influence of light on a hydrocarbon must be either polymerisation or oxidation or both. Before passing to substances where there is uncertainty as to constitution, experiments were made with some of the available non-oxidised hydrocarbon polymers.

A most convenient representative of this group is rubber. Rubber is known to yield the unsaturated hydrocarbon isoprene on destructive distillation, and in recent years it has been shown that it can be synthesised by the polymerisation of this hydrocarbon. The rubber used for many commercial purposes has undergone different kinds of treatment, *e.g.* vulcanisation, and contains in addition other constituents, but by the courtesy of the Ross Institute several samples of rubber in various stages of treatment were made available for this work. Three of these samples were made use of, as follows : " untreated crepe rubber," " pale crepe rubber," and " smoked sheet rubber." They were dissolved by gentle heating under a reflux condenser of 0·5 gm. rubber with 25 cc. gas oil, an oil which proved more suitable than the more aromatic medium kerosene extract. It did not seem that a higher concentration than this (2 per cent.) would repay investigation since this would probably be the limit for a practical proposition. The results showed that rubber was not an effective spread-aider. All three solutions were of about the same spreading pressure of 18 dynes/cm. Since it is not likely that the products formed by irradiation usually form a solution as strong as 2 per cent. yet give a spreading pressure considerably greater than this figure, it is reasonable to assume that they are not polymers of this type.

Another polymer which readily lent itself to investigation was polystyrene. The unsaturated hydrocarbon styrene or phenyl-ethylene is readily polymerised by simple heating, the complexity of the polymer varying with the conditions. For this work styrene was diluted with xylene until the styrene was only 10 per cent. of the whole. The mixture was gently heated under a reflux condenser for an hour. A simple experiment then showed that the involatile residue left on the surface of water was increased more than tenfold. But this nonvolatile matter had properties quite distinct from those of most substances forming unimolecular films on water. The difference was manifested when oil drops were added to the surface ; instead of the ordinary uniform spread, the oil moved in jagged streaks across the surface, obviously filling cracks in which there was no resistance offered to the oil. Observations with the Adam-Langmuir trough confirmed this, showing that the film though solid was unable to withstand lateral pressure ; the smallest pressure resulted in instability and crumpling of the film. The obvious way of interpreting this is to say that there exists no force anchoring the molecules of the film to the water interface, so that they form a sheet over the surface but do not offer any resistance to being displaced entirely from it. After this discovery it was not surprising to find that a solution of the polymerised product in oil did not greatly exceed the oil itself in spreading pressure. Dissolving the involatile residue in medium kerosene extract in the proportion of one to about seven by weight gave a solution of spreading pressure of only 13 dynes.

Simple polymerisation of hydrocarbons, without oxidation, does not therefore seem to lead to products contributing in any large degree to the spreading pressure.

5. *Oxidised polymerised hydrocarbons.*

The chief substance to be considered in this group is " cracked spirit gum." This substance has been referred to in the previous communication as one with the property of stabilising the film against the breaking action of wind currents, etc. Under certain conditions " cracked spirit," that is petrol prepared by the breakdown of higher boiling hydrocarbons through heating in a cracking unit, and containing a high proportion of unsaturated hydrocarbons, deposits this material spontaneously. It has been extensively studied since its presence in petrol causes considerable nuisance in internal combustion engines. Several authorities have agreed that it is the product of oxidation as well as of polymerisation ; thus Storey, Provine and Bennett (1929) state that it contains 20 per cent. of oxygen, while Brooks (1926) asserts that this oxygen is combined in the form of a peroxide. Researches by Flood, Hladky and Edgar (1933) and also by Martin, Gruse and Lowy (1933) have also established that the precursors of these gums are members of the class of hydrocarbons called conjugated diolefines, that is having the structure $-C{=}CH{-}CH{=}C-$ somewhere in the molecule ; chemists have for a long time recognised that this grouping leads to marked reactivity.

The fact that cracked spirit gum deposits itself from the petrol means that it only has a limited solubility in the other hydrocarbons. The material which has deposited it is found to have very active spreading properties ; the great rapidity with which a drop spreads out over the surface of clean water is a noticeable property, and the spreading pressure is found to be about 25 dynes/cm. In medium kerosene extract a saturated solution of cracked spirit gum was about a 3 per cent. solution and its spreading pressure was 23·9 dynes/cm. ; dilution to a half lowered this pressure to 21·1 and dilution to a quarter to 18·4 dynes/cm. so that this material was an effective and useful spread-aider.

Not all the samples of cracked spirit gum investigated were equally active. Very active preparations were obtained from a sample of " pressure distillate " from Burmah Oil Co., and from an olefinic petrol from Anglo-Iranian Oil Co., but a larger sample sent by request by the latter company, and received in the form of an acetone solution did not yield such an active product. This is hardly surprising since the series of consecutive reactions which make up polymerisation can lead to a bewildering complexity of products, which according to the number and position of the oxygen atoms introduced would have very different surface activities.

A sample of di-isobutylene (kindly supplied by Anglo-Iranian Oil Co). was investigated. This is a volatile unsaturated hydrocarbon of the formula $(CH_3)_3.C.CH{=}C(CH_3)_2$, boiling at 103°C. As it contains only one double bond it would not be expected to form gum. On storage, however, it undergoes chemical change, even in the dark, though faster in light. The freshly distilled substance evaporates from the surface of water leaving no residue, but the stored product leaves an invisible film, resisting compression in the ordinary way (whence unlike polystyrene). When the involatile residue was dissolved in medium kerosene extract the solution had a spreading pressure of 20 dynes/cm., and there was evidence that the maximum or plateau pressure was still higher. This suggests that oxidation is involved in the production of the substances, although this is not proved.

Cracked spirit gum, the product from di-isobutylene, and the product from ordinary oils under the influence of direct sunlight have properties in common and it may be that the differences are more quantitative than qualitative. This at present, however, can only be speculation.

6. *Sulphonated derivatives of oils.*

The last group of substances investigated in this section was the sulphonated derivatives of hydrocarbons. Their interest lies in the fact that treatment with sulphuric acid plays a part in nearly all methods of refinery, and sulphonated products might easily be responsible for some of the properties of commercial samples of oil.

Most of our knowledge of the sulphonated derivatives of the petroleum hydrocarbons we owe to Pilat and his co-workers Sereda and others, who working in Lwow, Poland, have fractionated and classified these bodies on the basis of their solubility and the solubility of their salts in water and ether. The first classification is into α, β and γ acids. The latter occur only in the acid layer, but of the two former, the α, while found principally in the acid layer are partly present in the oil layer, while the β are found principally in the oil layer, though in the acid layer after treatment with " oleum " (fuming sulphuric acid).

In this work samples of sodium sulphonates of hydrocarbons were obtained from the Shell Co. From the solubility relationships it appeared that their " A sulphonate " roughly corresponded with Pilat's β, and their " B sulphonate " with Pilat's α. The "A" was a golden wax-like substance soluble in oils but not in water, while the " B " was a brown powder soluble in water but for the most part insoluble in oils. A solution described as " Spreader B " appeared to be substantially the same as the material in the solid " B."

In the previous publication (pages 23–4) it was shown that the "A" sulphonate was unsuitable to add to oil because it led to an almost immediate break-up of the film. Even at that time, however, it was observed that the substance greatly raised the spreading power, and experiments were made to find the precise extent of this power, In medium kerosene extract 0·25 per cent. solution gave a spreading pressure of about 20 dynes/cm. and 1 per cent. solution gave 25 dynes/cm. Even this did not appear to be a maximum, and a 4 per cent. solution definitely spread against a pressure of 30 dynes/cm. This agrees with the observation already noted (page 214), that the monofilm formed by the material withstands compression of this order. The major difficulty in making measurements with this material was to find anything other than itself capable of being used as the buffering film.

The " B " sulphonate not being itself soluble in oil was treated with dilute hydrochloric acid as a first measure. In the case of the solution " Spreader B," this was marked by a great increase in viscosity and if left at this stage a tarry mass settled out at the bottom. The acidified fluid was then thoroughly shaken with oil or with light solvent, and the two layers separated. A hand-operated centrifuge was found convenient in the case of oil extraction. A rather curious fact was discovered at quite an early stage of this work. In the case of oil extraction, whether the oil was predominantly aromatic (medium kerosene extract) or almost wholly paraffinic (gas oil) a solution of extremely high spreading power was obtained. But in extraction with light solvent, a most remarkable difference was found between the action of benzene and of petroleum ether. The active substance is readily extracted by benzene but scarcely at all by petrol ether. This was shown first by the monofilm method (page 215) and confirmed by evaporation of the solvent and taking up the residue in oil. The petrol ether extracted a gummy material, but a 3 per cent. solution of it was required to give 20 dynes/cm., a 1 per cent. solution only having spreading pressure 14·7 dynes/cm. After four extractions with petrol ether subsequent extraction with either benzene or oil yielded the active material.

The oil solution obtained by shaking equal volumes of " Spreader B " and medium kerosene extract in the presence of acid had the highest spreading pressure then encountered, at least 40 dynes/cm., though defying accurate measurement. The pressure rises in direct proportion to the concentration up to 22 dynes/cm. (often a maximum figure for other substances), afterwards falling a little from linearity; as far as could be judged the curve never flattened to a " plateau " maximum.

One point of interest was noticed with both "A" and " B " sulphonates. When the solution in oil was added to a surface covered with a highly compressed film, there was a period of two or three seconds before the drop began to spread, but it then proceeded with acceleration, the resisting film being sometimes pushed right to the edge. The opposite of the effect described with cresol (page 221) can then be observed, for a second drop will remain unaltered while the first is still rapidly expanding.

The great difference between the two sulphonates in regard to the stability of the film after spreading was sufficiently commented upon in the preceding communication (Murray, 1938, p. 24).

As both the "A" and " B " sulphonates were only technical preparations it was considered desirable to confirm the observations by employing authentic products, *e.g.* synthetic preparations. It was also desired to distinguish between sulphonates and possible sulphuric esters. An example of the latter class of substance was made available through the courtesy of Messrs. Ronsheim and Moore, who kindly supplied a sample of sodium lauryl sulphate, a compound in which one of the acid groups of sulphuric acid is esterified with the 12 carbon-atom straight-chain alcohol, lauryl alcohol. Messrs. Bayer Products Ltd. kindly supplied a sample of a synthetic sulphonate of a paraffin hydrocarbon, a substance given the name of Igepon 702K, but the details of its composition were not made known. Both these substances were water-soluble white solids. They were known to be surface-active and to have soap-like properties. The suppliers of the samples in each case gave the opinion that the water-solubility of the substances would render them unsuitable for the aims of the present work, and this turned out to be true, although the experience with " Spreader B " had shown that a water-soluble salt could give rise to an acid which remained stable in oil solution in contact with water. The following experiments with sodium lauryl sulphate were made. An aqueous solution was made and acidified, there was no precipitate and the solution was then shaken with oil. An emulsion was thereby formed which proved extremely difficult to break. The aqueous layer was removed readily enough, but the upper emulsified layer was only rendered clear by shaking with a solid drying agent. Calcium chloride was avoided since calcium lauryl sulphate is insoluble and anhydrous sodium sulphate was therefore used ; after shaking the emulsion with this material it cleared and a true oil layer was obtained. Moreover this oil had a high spreading pressure, about 22 dynes/cm. in the undiluted state, and indicating from the dilution curve that this was not the maximum. On the other hand its behaviour after spreading was just that encountered with phenol and the other soluble substances, namely, the spread drops gradually contracted till they were no bigger than when first put on, and they would not then spread even if the pressure were released to a figure lower than that originally measured as the spreading pressure. The behaviour of the Igepon product was substantially the same. The solution of the acid in medium kerosene extract had a spreading pressure of 28 dynes/cm. In this case the dilution curve was found to be of unusual shape, for whereas the first additions of the material made only small increments in the spreading pressure, with further additions the increments became larger instead of progressively smaller as with nearly all the other substances investigated (Table X).

TABLE X.

Spreading Pressures of Solutions of the Acid derived from " Igepon 702K " in medium Kerosene Extract.

The concentrated solution was diluted with different volumes of the kerosene solvent.

Parts concentrated solution in 8 parts ...	—	1	2	3	4	5	6	7	8
Spreading pressure	10·6	12·2	13·4	15·0	17·7	19·9	21·7	25·0	28·0

After spreading the active material, however, diffused out of the oil into the aqueous layer and the drops contracted.

Evidently neither the 12 carbon chain of lauryl alcohol nor the chain in this compound is sufficiently insoluble to cause the molecules to anchor at the interface. The Shell spreader, although having a water-soluble sodium salt, must in its free acid form be scarcely soluble.

It is interesting to note that at the end of a simple hydrocarbon chain the $-SO_2OH$ group is more effective than any other grouping investigated, but the peculiar properties which make the Shell product such a suitable spread-aider depend on the structure of the rest of the molecule.

Influence of the Solvent on the Spreading Pressure of the Solute.

The values of spreading pressure recorded for different substances from page 218 onwards have, with the exception of the figures for rubber, referred to solutions in medium kerosene extract, a material mainly aromatic in composition, being the product of extraction with liquid sulphur dioxide. It was desired to investigate whether the solvent had any effect in determining the spreading pressure exerted by various solutes.

This question continues the subject discussed on page 215. Part of Adam's suggestion there quoted was that if there was great attraction between the molecules of solvent and solute, surface activity would be restricted and fall short of its potential maximum. Aromatic solvent would show greater attraction than paraffin, so the maximum spreading pressure would be lower in aromatic solvent. This was now found to be the case. When gas oil was the solvent the spreading pressure was regularly higher than that given by the same concentration of substance dissolved in medium kerosene extract. In the case of oleic acid the figures were very striking. Table XI shows them. The figures for medium kerosene extract are copied from Table VI, with those for gas oil beneath them. It may be pointed out that the gas oil, which had been subjected to further refinement since receiving it, as will be described in the next section, had itself a spreading pressure much lower than that of the medium kerosene extract, namely only 2·5 dynes/cm. Repetition of the measurements, using a sample which was the same gas oil treated in a different way and having a spreading pressure of 10 dynes/cm., gave figures not appreciably different. (The gas oil before treatment had a spreading pressure of 17 dynes/cm.)

TABLE XI.

Spreading Pressures of Solutions of Oleic Acid in Gas Oil and in medium Kerosene Extract respectively.

Percent. oleic acid	—	0·5	1·0	2·0	3·0	4·0
Spreading pressure (MKE)	9·0	13·2	13·8	14·5	—	15·9
„ „ (Gas oil)	2·5	13·9	17·8	20·2	21·7	23·7

Table XII gives results for cracked spirit gum obtained from the top cut of pressure distillate (Burmah O.C.). The upper line of figures is taken from page 224, the figure furthest right in the lower line by diluting the saturated solution in medium kerosene extract with three volumes of gas oil, and the remaining figures by further diluting with oil of the appropriate composition.

TABLE XII.

Spreading Pressures of Solutions of Cracked Spirit Gum in medium Kerosene Extract and in a Mixture of one part of that Oil with three parts of Gas Oil.

Concentration of gum (arbitrary units, saturated solution in MKE = 100)	4	8	12	16	25	100
Spreading pressure—						
(*a*) Medium kerosene ex.	—	—	—	—	18·4	23·9
(*b*) 1 MKE + 3 gas oil	15·4	18·5	20·2	22·1	23·0	—

One further example may be given. The spreader in this experiment was a product obtained from an anti-malarial oil (B.O.C. " Malariol," Assam formula) by extraction with aniline (see page 230). It was a rich brown viscous paste. Portions were weighed out and oil added to make 5 per cent. by weight. By mixing the strong solution with further quantities of the solvent the dilution curve was obtained. It will be seen from the figures (Table XIII) that both for medium kerosene extract and for gas oil this concentration was more than enough to raise the spreading pressure to the limiting figure, but that this limit is not the same for the two solvents. The material was completely soluble in medium kerosene extract but there were flecks of insoluble solid in the 5 per cent. mixture in gas oil which persisted until the dilution was about 1 per cent.

These results are obviously of considerable importance. Under conditions where spreading pressure was likely to be an important factor, and this would include any case where mosquito larvae congregated in shallow patches of water separated from the main expanse by floating vegetation, it would be uneconomical to allow potential spreading ability to be wasted through use of an unsuitable oil solvent.

The questions raised will, however, be more profitably discussed at the conclusion of this work, after the description of work showing methods of concentrating the active spread-promoters which already occur in oil.

TABLE XIII.

Spreading Pressure of Solution of a concentrated Preparation of the Spreading Factor from an Anti-malarial Oil, dissolved in medium Kerosene Extract and in Gas Oil respectively.

Percent. substance	0·42	0·83	1·67	2·50	3·33	3·75	5·00
Spreading pressure—							
(*a*) Medium kerosene ex.	15·4	18·8	22·6	23·9	—	24·5	25·4
(*b*) Gas oil	21·7	24·5	26·2	—	27·7	—	28·6

Separation and Concentration of the Spread-Promoting Substances occurring in Oil.

Reference was made in the introduction (page 213) to the two methods of approach to the problem of the nature of spread-aiders, the synthetic and the analytic. The preceding sections have dealt with the former. The latter, as already emphasised, is limited by the complexities of petroleum chemistry, but some progress has been made with the preliminary stage, the concentration of the active material and the demonstration that it is a substance only forming a very small proportion of the whole oil, by the simple methods of extraction with polar solvents and of adsorption.

Whatever the composition of the active spread-promoting constituent may be, and, indeed, however many different classes of substances participate in aiding spread, it is certain that they must all be " polar " substances, and it ought to follow that they should show a preferential solubility in polar solvents. In other words in all such processes as the Edeleanu process the spreaders should be concentrated in the same fraction as the aromatic hydrocarbons, the extract as opposed to the raffinate or unextracted residue.

The Burmah Oil Company, who took a particular interest in this part of the problem, kindly sent samples of raffinate and extract of pressure distillate bottoms prepared by the use of three separate extractants, liquid sulphur dioxide (ordinary Edeleanu process), furfural and chlorex. The results of the first measurements of spreading pressure made on them did not appear to support the expectations described, the figures being as follows (Table XIV) :—

TABLE XIV.

Spreading Pressures of the Raffinates and Extracts prepared from Pressure Distillate Bottoms by the use of various Extracting Agents.

Extractant	SO_2	Chlorex	Furfural
Spreading pressure raffinate	21·5	25·0	15·8
,, ,, extract	23·0	16·3	18·7

Those for chlorex extraction show a disparity in the wrong direction, while the other two fail to show an obvious concentration of the active substance. Another point at this stage unexplained is the smallness of both figures in the case of furfural extraction.

These results had been obtained however before the discoveries described in the last section of the different maximal pressures in different solvents had been made.

Once possessed of that information, it was obvious that viewed alone they might give a quite erroneous impression, and that what was required was a dilution curve with an inert paraffinic oil as the diluting agent. The results of this experiment for the extracts and raffinates from extraction with SO_2 and furfural are given in Table XV; the diluting paraffin was partially purified gas oil of Roumanian origin (the nature of this partial purification will be described later).

TABLE XV.

Spreading Pressures of Mixtures of the Oils of Table XIV with inert Paraffin (Roumanian Gas Oil).

Parts of PDB fraction	Parts gas oil	Spreading pressure			
		SO_2 raffinate	SO_2 extract	furfural raffinate	furfural extract
8	0	20·3	22·6	15·8	19·3
7½	½	—	—	—	21·7
7	1	19·5	24·9	—	23·4
6	2	19·3	25·1	14·5	25·0
5	3	18·0	25·8	—	—
4	4	16·3	25·6	12·8	24·0
3	5	15·6	25·6	—	—
2	6	13·7	24·7	11·3	24·8
1	7	11·3	23·4	—	24·8

The conclusions from these results are quite different from the ones that would have been drawn from Table XIV alone; they are, however, just the ones which were forecast in the opening paragraphs of this section. The raffinate, the hydrocarbons of which are for the most part paraffinic and probably resemble that of the mixture of extract with the largest number of volumes of gas oil, has a spreading pressure which is still lower than this most diluted extract. It seems reasonable to conclude therefore that it has an even lower content of the active material, in other words a good deal more than seven-eighths, probably between 90 and 95 per cent. of the active material became concentrated in the extract. This would apply to the first set of figures, the SO_2 extraction; for the furfural extraction the raffinate was even weaker in the spreading constituent. The lowness of both figures for the furfural fractions, which caused surprise at first, must then be accounted for by supposing that this solvent makes a much more complete separation, the raffinate being very weak in the spreader, and the extract being very weak in paraffinic hydrocarbons; this latter fact makes the undiluted extract rather low in spreading pressure but dilution brings it up to about the same maximum as the SO_2 extract.

None of the three solvents employed by the Burmah Oil Co. in the above fractionations were employed in the laboratory, but other solvents have been used. Any organic liquid which while miscible with aromatic hydrocarbons is immiscible with paraffins ought to prove capable of making the separation. A well-known liquid with these properties is aniline, for the immiscibility of aniline with paraffins in the cold is used as the basis of a rough method of estimating the proportions of aromatic and paraffin in a hydrocarbon cut. The B.O.C. product "Malariol" (Assam formula) was therefore fractionated with aniline, and the solvent removed with hydrochloric acid. The raffinate had a spreading pressure of only 13·9 dynes/cm. and the extract 24·3 dynes/cm. The high value of the latter agrees with the fact that aliphatic hydrocarbons have some solubility in aniline at room temperature. Other liquids were found, some from their recorded properties, some as the result of trial and error. Acetic anhydride was one which gave a satisfactory fractionation. It would be preferable on a large scale to find a method of removing the solvent without destroying it, but for small scale work (on 10 or 20 cc. oil) the two layers were poured into boiling water which hydrolysed the acetic anhydride ; in the case of the extract the watery layer was then fairly rapidly removed and the oil boiled with fresh water to avoid risk of decomposing any active material with acid. The observation that methyl alcohol is immiscible with paraffins was also recalled and it was found that this substance effected the separation quite well. Ethyl alcohol is less suitable but the preparation " cellosolve," a half anhydride standing midway between alcohol and ether ($C_2H_5.O.C_2H_4OH$) works much as methyl alcohol. Both these substances have the advantage that they are freely miscible with water, and thus very easily removed from the oil. In the paragraphs that follow a number of examples of the use of these solvents in connection with experiments on the spreading factors of one or another kind in oil will be described.

Firstly, it is clear that these methods, at least as so far described, will not serve to separate the active substances from aromatic hydrocarbons. Where there is any quantity of this type of hydrocarbon in the mixture, the use of these solvents will result in a strong solution of active principle in aromatics, but further purification will not be possible by this method. Certain experiments were tried with an aromatic oil of high spreading pressure using the water-miscible solvents methyl alcohol and cellosolve. To the clear mixture of solvent and aromatic 15 per cent. of water was added and the mixture well shaken. A small amount of oil separated out and was removed. Further water was then added by instalments and the oil which separated removed each time. After drying these portions of oil their spreading pressures were measured. They showed a progressive rise, indicating that although the first oil thrown out of solution contained very little of the spreader, the latter soon began to precipitate with the oil, and was not appreciably concentrated by the series of operations. It was assumed that the hydrocarbon constitution of each portion of oil was similar, since the experiment was carried out with a special oil sample (kindly supplied by the Burmah Oil Co. Research Department, London) claimed to be completely aromatic and free from paraffins.

On the other hand if oils of very low aromatic content but containing actively spreading constituents are extracted, a very concentrated solution of the spreaders should be obtained. In particular it seemed that this would be a profitable way to obtain a concentrate of the substance produced by irradiation of mainly paraffinous oils like gas oil.

The experiments described in the preceding paragraphs have dealt with the naturally occurring spreaders of quite unknown composition. Simple experiments proved that the active products of irradiation and also sulphonic spreaders show similar behaviour towards the polar solvents. Some irradiated gas oil possessing a spreading pressure of 24 dynes/cm. was extracted twice with acetic anhydride. After the solvent had been removed from the raffinate the spreading pressure was found to be reduced to 10·8 dynes/cm., about the figure the oil had had before irradiation. A similar experiment using methyl alcohol as extractant produced the same result. In the following experiment the oils extracted were not irradiated, but were samples of the gas oils as received directly from the Oil Companies. The Roumanian gas oil had a spreading pressure of 16·9 dynes/cm., and the cracked (Iranian) oil one of 25·6 dynes/cm. (Compare Table I, the slight differences may be accounted for by minor differences in conditions on the dates of the two experiments.) 25cc. gas oil was shaken with 25cc. methyl alcohol. It separated into two layers very readily. A good deal of coloured material passed into the alcohol layer on both the first and second extraction. The oil layer was poured into a shallow dish and soon methyl alcohol could no longer be smelled. The spreading pressures were found to be :— Roumanian, 9·1 dynes/cm., cracked, 14·3 dynes/cm. The latter was therefore extracted again, and the spreading pressure further brought down to 11·5 dynes/cm. The degree of " saturation " of the original oil in regard to the spreader was estimated by a dilution curve experiment mixing the original oil with the extracted oil ; the figures (for cracked gas oil) for two-thirds, one-half, one-third and one-sixth of its original strength were 24·5, 23·0, 21·7 and 19·1 dynes/cm. respectively. Meanwhile the methyl alcohol layers were evaporated down, but it was found that at a certain stage in the evaporation they began to separate into two layers ; evidently they contained oil as well as spreader, and this had limited solubility. In the case of the Roumanian oil the lower (oil) layer spread at 17·1 dynes/cm. ; the upper (alcoholic) layer, after the remaining alcohol had been allowed to evaporate, spread at 22·3 dynes/cm. This layer, however, concentrated into itself the whole of the small trace of aromatics in the original oil, and when it was diluted with the washed oil its spreading pressure went up, in fact after dilution with seven times its volume of washed oil a mixture of spreading pressure 25·0 dynes/cm. resulted. Its behaviour was thus similar to the extracts of pressure distillate bottoms.

Several experiments demonstrating the extraction of sulphonic spreaders could be cited. Obviously it was not possible by these methods to remove the sulphonic bodies from aromatic oils, but, as indicated on page 226, the constituent of " Spreader B " could be brought into solution in gas oil although not in light paraffins. A solution was made in Iranian gas oil of initial spreading pressure 10 dynes/cm. ; the solution spread at pressures round 30 dynes/cm. Some of the solution was subjected to two extractions with acetic anhydride ; after excess of the solvent was removed from the unextracted oil the spreading pressure was found to be reduced to 8·7 dynes/cm. The rest of the solution was extracted with cellosolve. In this case it was only necessary to wash the oil layer with cold water to remove traces of solvent, after doing this the spreading pressure was found to be 9·8 dynes/cm. In this experiment a further stage was possible. The cellosolve layer was mixed with more fresh gas oil and the whole well shaken with excess of water. When it separated into two layers, a lower cloudy aqueous layer and an upper clear oil layer, the spreader was found to be in the oil layer, that now having a spreading pressure of over 20 dynes/cm. This must be counted as an important observation, as by a very simple manipulation the actively spreading constituent has been transferred from one oil into another. This ought to provide a valuable weapon for the task of building up a good anti-malarial oil, for the important property of good spreading, if lacking in an oil of otherwise good qualities (toxicity, etc.) can be added without difficulty.

From the experiments which have been described earlier one would foresee that this is quite a general property capable of application with any oil. The spreaders can only be separated and concentrated from a paraffinic oil but they may be added to any kind of oil by this method. It is unnecessary to tabulate examples of other cases where this has been achieved.

Some other possibilities of separating and concentrating the actively spreading constituents have been investigated in a rather preliminary way. The possibility of extracting them with alkali was an attractive one, since if this means succeeded they would be freed from both aliphatic and aromatic hydrocarbons. Sulphonic acids, if the alkali salts were of the class soluble in water and insoluble in oil, should be brought out by this method. The other spreading constituents contain oxygen atoms that might have acidic properties, though we have seen that the effect of known carboxylic groups is not sufficient to account for their properties. Table XVI shows the effect of extracting certain oils with alkali (in the cold, but experiments with two of the oils showed that boiling with alkali did not produce any greater effect). While the results are very irregular they all show a slight fall in the value of the spreading pressure after extraction.

Most of the extracts were coloured and hence obviously contained some extracted matter. They were acidified and shaken with benzene when the coloured matter passed into the benzene. The solutions were tested for active material, both by the rapid monofilm method (page 215) and by evaporation and dissolving the residue in oil. It was instructive to find that even in the case of the last two oils where the fall in spreading pressure on extraction was least, the extract was rich in the active substance. When the material from the B.O.C. special aromatic kerosene was transferred to other oil, a solution of much greater spreading pressure than the original was obtained, 25·6 dynes/cm. even for medium kerosene extract. This strongly suggests another change of solvent effect, the nature of the original solvent not permitting the dissolved substance to make its spreading powers fully manifest. The Burmah Oil Co. were unable to suggest what this substance might be.

TABLE XVI.

Spreading Pressures of some Oils before and after Extraction with cold Caustic Soda.

Oil	Initial S.P.	Final S.P.
Medium kerosene extract	9·0	6·1
Ditto irradiated by diffuse daylight	24·3	16·3
Solar oil (Borneo), similarly exposed	17·2	15·6
"Boxol" (aromatic solvent spirit) similarly exposed to light	25·6	13·7
"Malariol" (Assam formula)	25·6	23·0
Special B.O.C. all-aromatic kerosene	19·0	16·9

Another method by which it was considered that the active substances might be studied in a state free from gross contamination from oil was the method of attempting the adsorption of the active substance on a solid. Of the wide variety of solid adsorbants which could be employed only one, fullers' earth, has been used. The results have proved very striking, although they have not succeeded in accomplishing the original aim. On the other hand they have absolutely proved the truth of the assertion which underlies all this work, that the spreading properties of an oil are determined by constituents which make up only a minute proportion of the whole. For several oils have been rendered completely non-spreading by filtration through fullers' earth.

The fullers' earth used was obtained from British Drug Houses and was marked "for adsorption purposes." It was packed tightly to a depth of about one inch in a Gooch crucible, and the oil filtered through under slight pressure. It is not claimed that this is either the best way or necessarily the most convenient way, for no others have been compared with it. When about 25 cc. oil was filtered through such a depth of earth in a Gooch of 1 cm. average cross-section, a considerable reduction of spreading pressure occurred, about equal or rather greater than that produced by extraction with solvents, *e.g.* gas oil (Roumanian or Venezuelan) of spreading pressure 17 or 18 dynes/cm. was reduced to about 6 dynes/cm. In order to determine how rapidly the earth was spent, a repeat experiment was done in which the oil was filtered 5 cc. at a time and then the most interesting observation was made that the first 5 cc. filtrate from gas oil was absolutely non-spreading. Later the raffinate from aniline extraction of pressure distillate bottoms was similarly filtered through fullers' earth. This oil was chosen because it should by its former treatment be free or almost free from aromatics, and yet it had still a spreading pressure of 15 dynes/cm. The first 5 cc. filtered in the way described however proved to be a non-spreading oil. The brown colouring matter was also nearly all removed by the filtration, the filtrate being a pale yellow fluid. It is evidently true then that paraffinic hydrocarbons are as a rule non-spreading liquids, and the fact that commercial grades of gas oil do in fact spread is due to impurities present only in very small amounts. It is probable that these impurities do not influence the properties normally set out in the specification and that the latter as ordinarily given conveys no information from which the spreading properties can be deduced.

In so far as the original aim of these experiments was to obtain the spreading substance free from oil, it was not achieved. Samples of oil were freed entirely from the spreading constituent but the recovery of the latter was not successful. The Burmah Oil Co. suggested the method of washing excess oil from the earth with cold petroleum ether and then extracting the solid with hot benzene in a Soxhlet extractor. By this method something undoubtedly passed into the benzene but when the benzene solution was tested the substance sought for was not found. In the case of a very actively spreading oil " spinex " (Edeleanu extract of spindle oil) the substance eluted gave to oil a maximum spreading pressure of 10·8 dynes/cm.

Monofilm experiments gave results not entirely devoid of interest, because the substances obtained from different oils might be characterised by their surface properties. Thus among the oils was a sample of pressure distillate bottoms from Anglo-Iranian Oil Co. which differed in many ways from the Burmah Oil Co.'s product, as it dried to a solid on exposure of thin layers. The material obtained from this oil by adsorption and elution gave a film which solidified (see page 215) at 18 dynes/cm. compression and although momentarily withstanding very high pressures (56 dynes/cm.) collapsed to about 20 dynes/cm. On the other hand the material obtained from irradiated gas oil by the same method formed the opposite type of film ; after reaching 22 dynes/cm. further restriction of the area did not lead to any rise in pressure and the film never went solid. The gas oil before adsorption, however, had spread at 30 dynes/cm. The results were repeatable, but it is questionable whether very much could ever be deduced from them, as the films are almost certainly not homogeneous.

Comparing the two methods of separating and concentrating the spreading substances, solvent extraction appears at present the more useful. It does not remove the spreaders with such completeness, *e.g.* no non-spreading raffinate has been produced by this method, but on the other hand it yields the desired constituents in a convenient form and one in which they are immediately available.

Conclusions.

The principal conclusion to be drawn from this work is that oils owe their spreading properties not to the nature of their hydrocarbons but to substances which may be classed as impurities, since they only make up a small fraction of the whole. Their nature is largely unknown, though sulphonated derivatives, oxidised polymers of olefines, and substances produced photochemically from apparently any class of hydrocarbons, may all contribute to the spreading power.

Next to be borne in mind is that the ordinary specifications of oil give no indication of the presence or absence of these substances. Some measurement of spreading pressure should be included when oil is intended for anti-malarial work. From the data here collected it is easy to devise a simple test requiring no apparatus. It has been shown that the unimolecular films given by some substances do not exceed a certain limiting pressure even when excess is spread. A " standard " resisting pressure can thus be set up by dipping a rod in the substance and touching the surface of water in a bowl with it. Castor oil should be a particularly favourable substance, a good quality product (tasteless medicinal) being quite cheap, while the pressure (16 dynes/cm.) is probably high enough to make the standard. A mineral oil spreading over water so treated could be accounted satisfactory ; an oil failing to spread would require improvement.

It has been shown that a wide range of spreading pressures is encountered. Oils containing substances such as pressure distillate bottoms would probably spread satisfactorily. Whether oils contain such products is largely determined by economic grounds. They have little marketable value and hence are cheap, but the same reason makes their transport uneconomic. In remote places it is common to blend anti-malarial oils on the spot from available market products, and these might easily be too much purified, so that they no longer contain the particular products that favour spread.

In a place where the choice of oils is limited, what can be done to improve oils which do not satisfy the standard? Some suggestions can now be made. Unfortunately the method of irradiation is hardly practicable. It might be asked, does not this method become automatically applied if the expanse of water receives sunlight? In small scale experiments in bowls it does not, or not in a satisfactory manner. A partially spread patch of oil is thick in the middle, thin at the edges. The results of exposure to light is that further spread occurs at the edges where the film becomes so thin that it is easily broken and has no penetrating power when the mosquito larva touches it; the bulk of the oil forming the central thick patch remains unaffected.

Passing to the method of improving spread by additions of other substances, we have seen that some of these do not merit their at present favoured position. Water-soluble substances such as cresol do not produce a lasting effect, and better things than vegetable oils can be found. Cracked spirit gum and certain types of sulphonates are the best of the substances studied. Neither of these, however, is available in a form convenient for rapid addition, and the use of concentrates produced by solvent fractionation might be the most convenient of all.

Concentrates are not suitable for use alone. This is not said because small quantities are sufficient to give the maximum effect, for this would only be an objection if they were expensive, which is unlikely, but there would be at least three positive disadvantages attached to the use of the concentrates as they stand. Firstly, owing to their lack of paraffins the full spreading potentiality is not achieved, thus defeating the main object. Secondly, it is very difficult to produce a uniform film from too strong a solution of spreader; the first drops falling on the water spread very rapidly to a thin film on which later drops remain as lenses and never become completely assimilated. Finally, concentrates where really good separation has been achieved (*e.g.* with furfural) are too viscous.

A content of between 10 and 20 per cent. of these concentrates in a mainly paraffinous oil would probably prove most suitable, bearing in mind that in the last paper it was shown that a mixture of aromatics and paraffins in proportions near to equality led to a danger of instability of the film, and that previously (Murray, 1936) it was shown that toxicity of an aromatic oil was little reduced by dilution with four volumes of paraffin.

To conclude, therefore, these concentrates from high-boiling residues or light-activated oils, cracked spirit gum, and the sulphonic acid derived from the water-soluble petroleum sulphonates (α-sulphonates in Pilat's terminology) can all be satisfactorily used as spread-aiders, and the choice can be left to convenience. The most potent is not necessarily the best, because it may leave a residue hindering a second application of oil.

Summary.

1. A method is described of using the Adam-Langmuir surface pressure trough for the direct measurement of the spreading power of oils against surface contamination.

2. Pure higher paraffins are non-spreading and pure aromatics have only a small spreading pressure. Commercial grades of oils owe what spreading pressure they have to impurities which are only present in small quantities and can be removed.

3. The spreading power of oil is greatly increased by irradiation of very thin layers of the oil. Even so, only a small fraction undergoes chemical change, the great bulk being recoverable with its original properties.

4. Straight chain fatty acids and alcohols only raise the spreading pressure of clean oil to a figure which is often already reached in a cruder product. There is some evidence however that a simple group such as –OH can produce a high

pressure if attached to the right hydrocarbon framework. Of the substances investigated the ones producing the greatest effect were the products of combined polymerisation and oxidation of olefinic hydrocarbons (cracked spirit gum) and the products of sulphonation of oils.

5. Substances soluble in water do not form good spread-aiders because they dissolve out of the oil which then contracts again if there is resistance to its spread.

6. The maximum spreading pressure exerted by a substance in oil solution is greater in paraffin than in aromatic oils.

7. When oil is shaken with a solvent which separates aromatics from paraffins, the spreading constituents, whether naturally occurring or added, pass into the aromatic fraction. Strong concentrates can be obtained in this way, and methods can be easily devised for transferring the active materials from one oil to another.

8. The spreading constituents can be entirely removed from oil by filtering it through fullers' earth.

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NATURAL CONTROL OF *DIPRION SIMILIS*, HTG., IN POLAND DURING 1936.

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Introduction.

For several years Farnham House Laboratory has been studying large infestations of *Diprion* species on the European Continent in order that parasites of this species may be sent to Canada in an endeavour to establish biological control over the White Spruce Sawfly, *Diprion polytomum*, Htg. In 1937 the writer investigated a heavy infestation of *Diprion similis* on pine at Orle, near Wlosclavek, in Poland, from where over four million sawfly cocoons were shipped by Farnham House Laboratory to Belleville, the parasite laboratory of the Canadian Entomological Service, which is effecting the introduction of new species of parasites. The status of the infestation was both interesting and peculiar inasmuch as the overwintering sawfly prepupae did not proceed with development but remained in a prolonged diapause of more than one year's duration. During the course of the work it was possible to obtain some insight into the factors which were controlling this infestation and reducing it to negligible proportions. The complexity of these factors made it a matter of extreme difficulty to isolate individual effects with any certainty, but by using the evidence available, an attempt has been made to assign approximate values for each class of control.

Notes on the General Biology of Diprion similis, Hartig.

The adults of *Diprion similis* and *Diprion pini* are morphologically very similar and externally possess almost no diagnostic differences ; to circumvent the difficulty of separating the two species certain entomologists, such as Reh (1913), have suggested that *similis* is synonymous with *pini*, a theory which is hardly tenable in view of the distinctive differences of the immature forms. Baer (1906) has made a study of the " saws " of *Diprion* species, and has concluded that *similis* and *pini* may be separated by the differences in shape and uniformity of the teeth on that organ. The difficulty in the determination of *Diprion similis* and its comparative infrequency as a major pest are, no doubt, responsible factors for the paucity of literature on this species.

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[illegible] in 1937 [illegible]

on ~~[illegible]~~ [illegible] the [illegible]

[illegible]

work done in 1936 requires to be altered)

On the European Continent, *Diprion similis* has usually two generations, the larvae of the first feeding from the end of May until some time in July, and those of the second in August and September ; the development is greatly affected by the prevailing temperatures and no definite time for the appearance of a particular stage can be stated with certainty.

The spring adults emerge from their cocoons early in May and proceed to copulate approximately one day later. The males emerge at the same time as the females and do not pass through a maturation period as is usual with most other members of the Diprioninae. The females lay their eggs generally in the needles of the previous year's growth, the average number in a needle being six ; the female commences operations at the proximal end of the needle, facing the tip, and a fresh incision is made for each egg, which is, however, laid in close juxtaposition with the others ; during the process of oviposition the concentration of the adult is intense and the shoot can be removed from the branch to be examined at leisure without disturbance of the sawfly.

The eggs are of a bluish colour and, although separated from each other by a wall of plant tissue, they are so closely packed that their form is that of cubes with rounded corners ; the developmental period of the embryo is approximately 14 days, dependent upon the prevailing weather. A few days before eclosion the eggs assume a darker colour and the embryo can be seen lying curved within the envelope. Upon emergence from the egg, the young larvae feed on the outer edge of the needles, but later in life the whole needle is attacked and only the base remains. The distinctive larva of *Diprion similis* has been adequately described by Middleton (1923) and here it is only necessary to state that the shining black head and the body flecked with black and yellow in a fairly regular pattern form characters which easily distinguish it from other immature forms of sawflies which are to be found feeding on pine. The female-producing form has six larval instars and the male five before the prepupal stage is entered (Middleton, 1923). The prepupa does not feed but seeks a suitable place to spin the cocoon within which it will pupate ; on the European Continent the cocoons of the first generation are spun underneath or on the forest cover. In North America this differentiation in the location of spinning of the two generations is not observed and the cocoons of both are spun in the foliage (Hartley, 1923).

Normally the prepupal stage of the first generation is unmarked by any diapause and the developmental period between the spinning of the cocoon and the emergence of the adult is two to three weeks. The second generation prepupae enter a diapause in which they pass the winter, finally maturing and emerging as adults in the early spring. Under certain conditions, which are not yet known, a diapause of a few weeks may occur in the first generation life-cycle, while that which normally occurs in the over-wintering second generation may be prolonged for several months or even years. This interposition or lengthening of the diapause has been observed in *Diprion sertifer*, *D. pini* and *D. polytomum*, and thus appears to be a characteristic of the family.

This paper records the observations made on an infestation of *Diprion similis* in which 90 per cent. of the second generation prepupae, originally spun up in the autumn of 1935, remained in a long diapause for more than one year.

Natural Control of the Polish Infestation.

The infestation at Orle was visited at three periods during the year—April, June and October. During the October visit a large sample of cocoons was collected and stored at Farnham House in open trays placed in an insectary which was at outside temperature and open to outside air. This sample was dissected in December and the observations at this period are, therefore, not strictly true field observations and must be accepted with a certain amount of reservation.

Predators.

During the winter diapause the sawfly is in the prepupal stage, contained within the cocoons which lie scattered over the forest floor ; although they may be superficially concealed by a covering of sphagnum moss or pine needles they offer an unresisting and easily found objective for predators in search of food.

The most important predators were the shrews and voles which abounded in the forests ; these animals pierce the cocoons with their teeth, generally in the terminal region and suck out the entire contents, of which no trace is left. Besides the individuals which are destroyed in this manner, many cocoons were to be found on which the teeth-marks were plainly visible but through which no complete puncture had been made ; in the majority of these cases the larva had evidently suffered a certain amount of bruising, for it was nearly always found dead within the cocoon.

Besides vertebrate predators, a certain number of the sawfly prepupae were destroyed by Elaterid larvae and also by *Calosoma sycophanta* adults. It has not been found possible to separate with complete certainty all the cocoons which had been damaged by the mammals and those destroyed by the Elaterids, for the hole made in the cocoon by both classes of predator is very similar. From samples examined it was estimated that over 95 per cent. of the destroyed cocoons had been eaten by the shrews and the voles, and therefore the control exerted by the invertebrate predators was very small.

In some districts the action of predators was so efficacious that the infestation was quashed in the winter immediately following the spinning of the cocoons. Such an example was found at Margonin, near Posen, where it was extremely difficult to find any sound cocoons. At Orle, Wloslavek, where the infestation was studied throughout the year, the predators accounted for 46 per cent. of the *D. similis* population throughout the winter months of 1936–37. Although the remainder of the cocoons lay on the forest floor throughout the following summer, this figure did not increase to any appreciable extent, and it appears probable that the predators only consume the sawfly prepupae when other food is scarce.

Pathogenic Organisms.

Pathogenic organisms proved to be the most efficacious factor of control, and largely killed off the huge population of the prepupae in diapause. It is not known whether bacteria or fungi were the primary parasites, but while a certain number of the Tenthredinid was killed off by fungi (*Isaria* spp.), it is believed that the majority first succumbed to bacterial attack and were later infested by saprophytic fungi. In the majority of cases the onset of disease is denoted by brownish black patches appearing on the abdominal tergites and tarsi ; the prepupa may live several weeks after the first development of the symptoms, but in all cases it inevitably perishes.

The progress in mortality occasioned by these pathogenic organisms was studied by dissecting samples of cocoons in April, June, October, and finally in December. The first dissection demonstrated the mortality which had been occasioned throughout the winter of 1936–37, and at that time it was expected that the survivors would emerge in the normal way for the spring flight. This emergence did not take place and the progress of the bacteria and fungi was able to proceed throughout the prepupal population during the entire summer. The results found from the analyses of many thousand cocoons are given below :—

TABLE I.

Disease mortality of prepupae surviving the attacks of predators

	April	June	October	December
Percentage mortality	37·4	67·3	73·3	86·1

It is obvious that the time factor had considerable influence on the increase of mortality ; this is important when considered in connection with the abnormal length of diapause experienced by the prepupae. If a normal spring emergence of sawfly adults had taken place, the reduction in population would have been confined to 37·4 per cent. ; by the continuance of the diapause the suppression of the infestation was incurred, for the pathogenic organisms then proceeded to attack the majority of the winter survivors.

In general the diseased cocoons were filled with such a mass of fungal hyphae or putrified liquid material that it was impossible to ascertain what proportion of the dead prepupae had been parasitized by insects. There was, however, sufficient evidence to show that large numbers of the parasites had succumbed to the pathogenic organism, and observations described later indicate that in certain circumstances sawflies already parasitized by insects suffer even more heavily from bacterial and fungous enemies than do unparasitized individuals. Comparatively little is known concerning the diseases of prepupae and pupae which are enclosed within a resisting cocoon. It has been demonstrated that the cocoons of the Diprioninae are resistant to water and to changes in atmospheric humidity (Ullyett) ; also, it was observed that in the majority of cases the diseased prepupae had apparently sound cocoons, free from fungous hyphae. It therefore appears probable that the bacterial and fungous spores are present when the sawfly larva spins its cocoon and that these develop under suitable conditions which may entail a loss of resistance on the part of the host.

Parasites.

The parasite population was followed throughout the year both by dissections of the host and by the rearing of samples. In May and June there was an emergence of 90 per cent. of the parasite population, the remaining 10 per cent. persisting in diapause for the rest of the year. A list of the parasites which were reared from *D. similis* is appended below. Those marked with an asterisk have been previously recorded from this host.

		Stage of Host attacked
HYMENOPTERA :		
Ichneumonidae:		
Cryptinae :	*Spilocryptus adustus*, Grav.	Prepupa in cocoon.
	Microcryptus basizonius, Grav.	Prepupa in cocoon.
	Microcryptus subguttatus, Grav.	Prepupa in cocoon.
	Leptocryptus pellucidator, Grav.	Hyperparasite.
Ophioninae :	*Mesochorus* spp.	Hyperparasite on larval parasites.
Tryphoninae :	*Exenterus marginatorius*, F.	Larva.
	Exenterus laricinus, Thoms.	Larva.
	Hypsantyx impressus, Grav.	?
CHALCIDOIDEA :		
Pteromalidae :	*Eutelus subfumatus*, Ratz.	Prepupa in cocoon.
	Dibrachys cavus, Walk.	Hyperparasite.
Torymidae :	*Monodontomerus dentipes*, Boh.* ...	Prepupa in cocoon.
Eulophidae :	*Microplectron fuscipennis*, Zett.	Prepupa in cocoon.
	Tetracampe diprioni, Ferr.	Egg.
DIPTERA :		
Tachinidae :	*Sturmia inconspicua*, Mg.*	Larva.

The results of the sample dissections taken at four periods of the year are expressed below in Table II. The smallest sample contained 400 cocoons.

TABLE II.

Percentage parasitism of Diprion similis.

	Percentage parasitism of prepupae escaping attacks of predators or disease	Percentage parasitism of all uneaten cocoons, *i.e.*, including diseased prepupae
April	16	10
June	49·7	16·3
October	54·9	14·7
December	33·3	4·7

As many of the parasitic species involved have very similar larval morphology, it was not possible to separate the individual species by dissection. However, observations were made on the variation in populations of the Ichneumonids and Chalcids and these form interesting contrasts. The data are expressed in fig. 1.

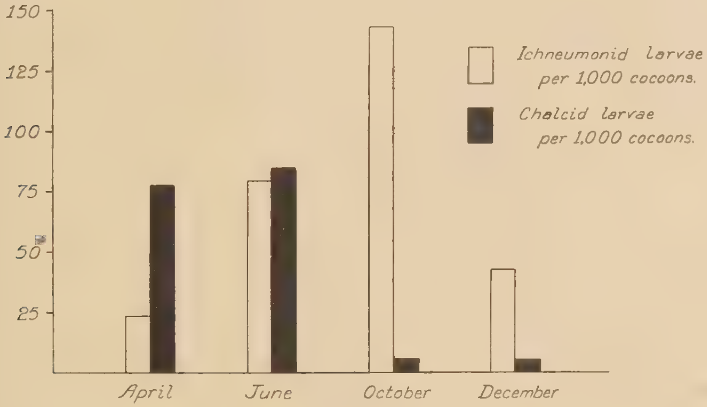

Fig. 1. Populations of parasite larvae in *D. similis* during 1936.

At the commencement of the warmer weather at the beginning of May the Chalcids, consisting largely of *Microplectron fuscipennis*, emerged first and began immediately to oviposit in fresh hosts. Under favourable conditions the life-cycle of *M. fuscipennis* can be as short as ten days, and it appeared probable that the Chalcid population would steadily increase throughout the summer, as the host supply was so numerous. Instead, the population increased to a peak point (representing 8 per cent. parasitism of cocoons with living contents) in June, after which there was a rapid fall to almost negligible proportions.

The beginning of emergence of the Ichneumonids was slightly later than that of the Chalcids, and instead of being confined to a period of approximately ten days, was spread over a period of one month. By June the Ichneumonid population had only increased slightly, but by the end of October a 100 per cent. increase in the population had been obtained. It is important to notice that the drop in population which occurs after October must be correlated with a mortality due to pathogenic organisms and not to a true reduction in population, as in this period *no* emergences of parasites were recorded.

A tentative explanation may be put forward to account for the surprising drop in the Chalcid population experienced in the middle of the season. In June 1937 Poland experienced a record-breaking period of heat in which temperatures rose above 40°C. Now according to Ullyett (1936) *Microplectron fuscipennis* adults, the chief Chalcids involved, have a zone of inactivity between 35–40°C., the latter temperature being lethal. It is suggested that the great heat was fatal to the Chalcids and accordingly reduced their numbers. The survival of the Ichneumonids may be due to intrinsic qualities or to their later and lengthened emergence period.

Inter-relation of the Biotic Controlling Factors.

In the estimation of the value of controlling factors often too much reliance is placed on the purely observable data which are obtained by direct observation in the field, whereas it is obvious that the mutual interference of the various factors concerned result in a complex in which individual rôles can only be interpreted when a certain amount of inductive reasoning is applied to the direct observations. When considering host-parasite complexes with a view to the selection of factors for use in biological control in another area, it is especially important that individual rôles be determined.

For purposes of convenience the data obtained directly by observation are set out in Table III. The figures are taken from random samples of cocoons which *include* those destroyed by predators and those from which parasites emerged ; hence values for disease and parasitism are proportionately lower than those given in Tables I and II.

TABLE III.

Field data on the fate of D. similis *cocoons at Orle, Poland.*

	Percentage eaten by predators.	Percentage mortality due to pathogenic organisms	Percentage cocoons containing parasite larvae	Percentage cocoons from which parasites emerged	Percentage healthy unparasitised sawfly prepupae
April ...	46	20·2	5·4	0	28·4
June ...	46	33·1	8·0	4·8	8·1
October ...	46	36·6	7·2	4·8	5·4
December ...	46	42·4	2·3	4·8	4·5

As the host population, i.e. *Diprion similis*, remained stationary throughout the year, the interpretation of the data is much simpler than in the usual cases where the host population is increasing.

The action of the predators was confined to the winter months and accounted for 46 per cent. of the sawfly population. This value remained fixed for the complete year.

As has already been stated, the external appearance of the sawfly cocoon is no guide indicating whether the contents are healthy or diseased, and it is thus unlikely that a predator can recognise those cocoons containing diseased prepupae without first biting them and making the characteristic ragged hole ; furthermore, the disease factor increased with time (Table II), while the attacks of predators occurred in the first few months. It is therefore probable that predators consume both hosts which would have eventually perished through disease and also open cocoons of already diseased prepupae.

Thus, when considering the effect of pathogenic organisms some modification must be made in the values given in Table III. In April dissection of a random sample containing both eaten cocoons and full cocoons showed that 20·2 per cent. of the prepupae were destroyed by fungus or bacteria. This figure corresponds to a destruction of 37·4 per cent. of the cocoons which had escaped the attacks of predators, and it must therefore be assumed that an equal percentage of those cocoons which were eaten would have succumbed to similar disease. Therefore the true valuation of the pathogenic organism control for April must be expressed as 20·2+17·2 (37·4 per cent. of 46)=37·4 per cent.

Now this concealed 17 per cent. of potential control remains constant for the rest of the year, as neither fungus nor bacteria can increase in empty cocoons and the predators had already ceased their destruction in April. Thus the value of the pathogenic control for June is also the observable percentage value plus the concealed 17 per cent., *i.e.* 33·1+17·2=50·3 per cent. In a similar manner the remaining figures for October and December must also be increased by 17·2 per cent. to show the complete potential control.

In considering the control which would have been exercised by parasites in the absence of other controlling factors, no effort has been made to calculate the loss in reproductive capacity of the parasite population occasioned by the premature death before oviposition brought about by predator or time. An endeavour has been made to calculate the number of hosts which contained parasite larvae or eggs and must have inevitably perished through their agency if no other fate had intervened.

To make such calculations it has been assumed that pathogenic organisms attack parasitized and unparasitized *Diprion* prepupae with equal readiness ; this assumption will be discussed later in this paper.

In April, 16 per cent. of the cocoons containing living contents were parasitized, and it must therefore be assumed that 16 per cent. of both eaten and diseased cocoons also contained the same percentage of larvae or eggs. The total percentage of parasitized prepupae is thus represented by the following summation : 5·4 (living parasites)+7·4 (16 per cent. of eaten cocoons) +3·2 (16 per cent of diseased cocoons) =16 per cent.

Now in considering the parasite factor for June, it is obvious that the parasite content cannot have increased or decreased in the cocoons which had already been diseased or eaten away at the time of the April observation. Those prepupae which succumbed to disease after April will, however, contain the same percentage of parasites as the cocoons with living contents, *i.e.* 49·7 per cent. Thus the parasite population with reference to living larvae and prematurely killed individuals can be calculated as follows :—

	Per 100 host Cocoons
(1) Living parasite larvae (by dissection)	8
(2) Parasites killed by predators during the winter	7·4
(3) Parasites killed by disease up to April	3·2
(4) Parasites killed by disease between April and June	6·4
	25·0 per cent.

Now in April and May 90 per cent. of the living parasite population successfully emerged as adults, and therefore those parasite larvae which were found in June and onwards belong for the most part to a distinct and later generation. Thus the total percentage of parasitized hosts up to June is equal to the summation of the living parasite larvae and prematurely killed larvae plus the number of successful emergents. When expressed in percentages, therefore, the number of parasitized hosts up to June was 25·0+4·8 (90 per cent. of 5·4)=29·8 per cent. The values for the recurring two periods of the year were calculated in a similar manner and the complete figures are set forth in Table IV.

TABLE IV.

Calculated effect of controlling factors after eliminating natural interference.

	Percentage destruction by predators	Percentage destruction by disease	Percentage destruction by parasites
April	46	37·4	16
June	46	50·3	29·8
October	46	53·8	30·9
December	46	59·6	27·9

It will be noted that in column 4 of Table IV an apparent decrease in the controlling effect of parasites is shown in the period October–December. As the figures for each observation represent a summation of controlling action up to that point, it is, of course, impossible for an actual decrease to have taken place. This apparent reduction may be explained by reference to Table III which shows that, while the increase in disease mortality is exactly balanced by the loss of parasites and healthy host pupae, the mortality of parasitized prepupae was much greater than that of healthy prepupae. Thus for the period October–December, the assumption that parasitized and unparasitized hosts are attacked by pathogenic organisms was incorrect ; however, in the period June–October the mortality due to disease of unparasitized hosts was *less* than that of parasitized, and therefore it is not possible to attempt further modifications of the data so far presented.

However, it appears probable that hosts which have been attacked by parasites are more likely to succumb to disease than healthy hosts, as the resulting weakness and final disintegration brought about by the parasite larva must be favourable to the growth of bacterial or fungous spores. In basing the calculations upon the assumption that parasitized and unparasitized hosts are equally vulnerable to pathogenic attacks, the writer believes that the *lowest* estimate for the parasitized individuals has been obtained and that the actual figure is probably higher.

The highest figure in column 4 of Table IV must be taken to represent the percentage of hosts which were parasitized and which have inevitably perished even though they had survived the action of the two other controlling agents.

Other disadvantages in the method of calculation presented lie in the fact that the control of the host prepupae is a continuous phenomenon and cannot be divided up into sections without the introduction of errors. Nevertheless, it is believed that the picture of the biotic controlling factors is more adequately represented by results obtained in this manner, even though approximate, than the bare data observable directly in the field. Figure 2 is a diagrammatic representation of the actual and calculated control exercised by predators and pathogenic organisms, and also depicts their mutual interference. The complete square represents the total population of sawfly prepupae which spun up in the autumn of 1936. The shaded areas represent the proportion of hosts which were destroyed by the various controlling agents.

Comparison of Tables III and IV shows that the superiority of the predators over parasites shown by field data is more apparent than real ; while 46 per cent. of the host population was destroyed by predators, at least 30·9 per cent. of the hosts contained parasites and would have inevitably perished. In spite of the fact that the parasite estimation is probably too low and the disease figure too high, the control exerted by pathogenic organisms appears to be really superior to that exerted by predators or parasites ; this may be partly explained by the fact that the fungous and bacterial diseases were able to progress continuously, while the action of predators was cut short in the spring, and any increase in parasitism was confined to a single period of multiplication when the adult parasites were depositing their progeny in May and early June.

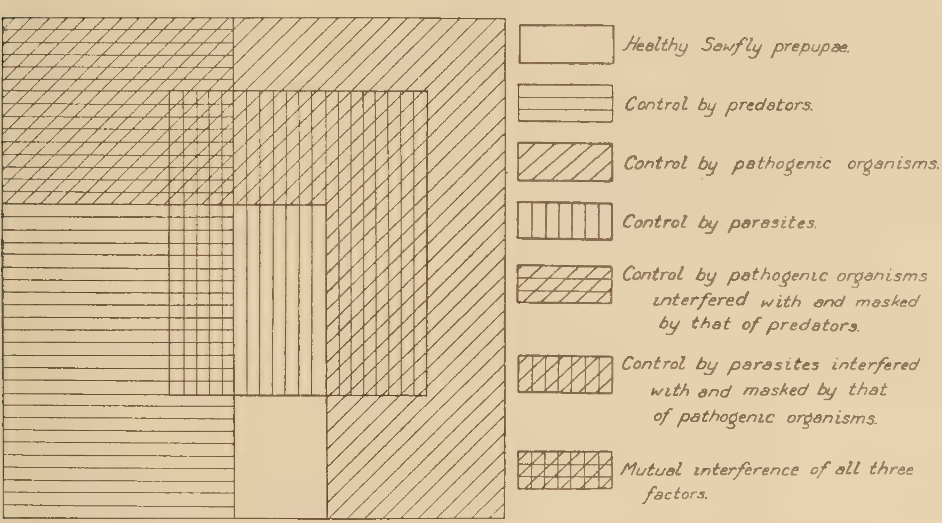
Healthy Sawfly prepupae.
Control by predators.
Control by pathogenic organisms.
Control by parasites.
Control by pathogenic organisms interfered with and masked by that of predators.
Control by parasites interfered with and masked by that of pathogenic organisms.
Mutual interference of all three factors.

Fig. 2. Graphical illustration of the fate of the *D. similis* population in Poland from October 1936 to December 1937.

The infestation which was under review cannot be regarded as a typical sawfly infestation, as conditions were apparently unfavourable to the development of Hymenoptera—both host and parasites. It is thus difficult to draw conclusions concerning the effective control of parasites from this single example, but from investigations by the writer at Orle, Gnievokowo, Margonin and Porzecze, it is probable that parasite control always has a minimum of 15 per cent. in the first parasite generation and 30 per cent. in the second. The most constant control is applied by predators, chiefly vertebrates, and in favourable conditions is so severe that complete suppression of the infestation ensues. Little is known concerning the control exerted by pathogenic organisms on *D. similis*, beyond the example quoted in this publication, but from observations on fungous and bacterial diseases of other species of DIPRIONINAE, it is probable that such control is sporadic, occasionally being severe, as at Orle in 1937, but often of minor significance. Where the action of predators or disease reaches high proportions, the possible controlling effect by parasites is considerably masked.

Summary.

During a search over Europe for species of the genus *Diprion* an infestation of *Diprion similis* was located in Poland at Orle, near Wlosclavek. The infestation was remarkable in that the prepupae which had spun up in the autumn of ~~1935~~ did not proceed with normal development in the following year, but remained in a prolonged dispause. An opportunity was thus afforded of studying at length the control exerted by biotic factors on the prepupal stage of the host sawfly.

[illegible]

By field observations and dissections it was discovered that predators had killed 46 per cent. of the sawfly population during the winter ; their attacks were not continued during the summer months. Pathogenic organisms proved to be a most efficacious factor of control, for the disease mortality of sawflies surviving the attacks of predators rose from 37·4 per cent. in April 1936 to 86 per cent. in the following December. Parasitism of the survivors of both predators and pathogenic organisms rose to its highest peak in October, when 54·9 per cent. was recorded.

At the commencement of warmer weather the population of Chalcid parasites increased rapidly but suddenly fell to negligible proportions after June, while that of the Ichneumonids continued to rise steadily. It is suggested that the great heat experienced in the early summer months resulted in the death of the Chalcids.

By consideration of the field data an attempt is made to separate the effects of the various biotic controlling factors and to assign to them approximate numerical values. The actions of these factors largely overlap each other, with the result that the effect of an individual factor is minimised to a certain degree. Approximate values are calculated for the destructive action of each factor after eliminating interference by other factors, and these conclusions, together with the degree of interference are set out graphically in fig. 2.

Acknowledgments.

I am indebted to Dr. W. R. Thompson, F.R.S., for his sympathetic criticism of this paper, and my thanks are also due to Dr. Marjan Nunberg, of the Institut Badawczy Lasow Panstwowych, for the facilities he provided for me in Poland.

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ON THE PERIOD OF SURVIVAL OF THE EGG, LARVA, AND FIRST NYMPH STAGES OF THE ARGASID TICK *ORNITHODORUS MOUBATA*, MURRAY, AT DIFFERENT RELATIVE HUMIDITIES.

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Introduction.

This is part of an investigation intended to cover all stages of this tick at different temperatures as well as different humidities. It has been found that the work will take a long time to complete, and it was therefore thought worth while to publish this portion of it separately, particularly as the results do not agree with those of previous workers.

It is well known that this tick is capable of living without food for a very long period (Newstead 1905, Symes 1926 & 1927, Cunliffe & Nuttall 1921, and others), but the conditions necessary for this survival do not appear to have been investigated at all thoroughly. Colas-Belcour (1929) and Rodhain (1919) consider that this tick is favoured by a low humidity, and Rodhain suggests their high humidity as a reason for its absence from equatorial forests. Cunliffe (1921) in laboratory experiments found that the length of life was lowered by an increase in temperature. He also experimented on the effect of different degrees of humidity. At 30°C. he found that a saturated atmosphere, obtained by having excess water in a covered jar, was extremely unfavourable to the survival of this tick. A " moist " atmosphere, obtained by sprinkling a few drops of water in the jar every day was less unfavourable, but the most favourable conditions were " dry," obtained by having a layer of calcium chloride crystals in the bottom of the jar. Under these conditions 66 per cent. of the 1st stage nymphs with which he started reached the adult stage, and all lived for a much longer period than under the other sets of conditions.

This investigation is an attempt to discover more exactly the influence of temperature and humidity on the longevity of this tick when unfed and the conditions tending to reduce it to a minimum.

Method of Experiment.

The method adopted for this experiment was to place ova in desiccators containing sulphuric acid to produce different humidities, and to note the metamorphosis and numbers dead and alive at intervals of a few days. The details were as follows.

The female parents were bred from ova and kept at 25°C. in dry sand and at uncontrolled but fairly high relative humidity all through their development. Six females were used, and the ova they deposited during a period of two days at the time when they appeared to be ovipositing at their maximum rate were used for this experiment. Jobling (1925) has observed that a female can lay six batches of eggs, each after a meal, but that the percentage of eggs capable of development gradually declines in successive batches. It was therefore thought advisable to take the precaution of using only first batches for experimental work, and this was done. Jobling found that, on the average, 96·8 per cent. of the eggs in first batches developed, and using this figure, it may be assumed that a negligible proportion of the mortality described below was due to non-viability of the eggs.

The ova from each female were divided into eight batches as nearly equal as the numbers would permit. Each batch was placed in a shallow filter paper cup in a $2 \times 1\frac{1}{2}$ in. tube, and one batch from each female was put into each desiccator, the tubes all being left open at the top. This was done in order to eliminate the effect of possible differences of resistance to desiccation of the progeny of different females. A detailed examination of the results of the experiment showed that this was a necessary precaution, but the numbers were too small for it to be possible to publish significant figures. The ova were examined the following day, and the only one that was already shrivelled was discarded as having been damaged in the transfer. A day or two previous to this, sulphuric acid solutions of specific gravities to produce the required relative humidities had been placed in the desiccators. The specific gravities were checked again at the end of the experiment, and were found to have altered by a negligible amount. The specific gravities of sulphuric acid used, the theoretical relative humidities produced by these solutions, and the specific gravities as checked at the end of the experiment, are given in Table I.

TABLE I.

Specific gravities of solutions of sulphuric acid used in desiccators, and theoretical relative humidities produced by them

Desiccator No.	1	2	3	4	5	6	7	8
Sp. Gr. of H_2SO_4 at 15°C. ...	1·198	1·249	1·293	1·337	1·432	1·485	1·554	1·600
R.H. % theoretically produced at 25°C.	80	70	60	50	30	20	10	6·2
Sp. Gr. of H_2SO_4 at end of experiment	1·199	1·249	1·293	1·337	1·430	1·484	1·550	1·596

TABLE II.

The number of ova from each female tick placed in each desiccator, and the totals from each female and in each desiccator

Desiccator No.	Batch Letter						Total ova in each desiccator
	A	B	C	D	E	F	
1	8	6	6	9	9	9	47
2	8	6	6	9	9	10	48
3	8	6	6	9	9	9	47
4	9	6	6	9	9	10	49
5	9	6	7	10	9	10	51
6	8	5	6	9	9	9	46
7	9	6	7	10	9	10	51
8	8	5	6	9	8	9	45
Total ova used from each ♀	67	46	50	74	71	76	384 = Total used in experiment.

Table II shows, in vertical columns, the distribution of ova from each female tick in the different desiccators and the totals, and in horizontal lines, the source of each batch of ova and the total number in each desiccator.

TABLE III.

The ages and stages in which the ticks died at the different relative humidities

Desiccator	Rel. Hum. %	1st day	2nd day	6th day			10th day			13th day				18th day					21st day				24th day			
		Ova	Ova	Ova		La	Ova		La	Ova		La	Ny	Ova		La		Ny	La		Ny		La		Ny	
				D	A	A	D	A	A	D	A	A	A	D	A	D	A	A	D	A	D	A	D	A	D	A
1	80	47	47	—	42	5	—	10	37	—	—	34	13	—	—	—	—	47	—	—	—	47	—	—	—	46†
2	70	49	48*	—	45	3	—	7	41	—	—	34	14	—	—	—	—	47†	—	—	—	47	—	—	1	46
3	60	47	47	—	45	2	—	19	28	1	—	38	8	1	—	1	—	45	1	—	—	45	1	—	—	45
4	50	49	49	1	41	7	1	14	34	1	—	37	11	1	—	—	1	47	1	—	1	46	1	—	1	46
5	30	51	51	2	49	—	9	15	27	11	—	36	4	11	—	—	11	29	4	4	—	32	7	—	—	33
6	20	46	46	2	40	4	6	22	18	15	2	23	6	17	—	—	13	16	9	2	—	18	9	1	—	19
7	10	51	51	3	48	—	21	13	17	25	3	22	1	28	—	—	15	8	6	6	—	11	12	—	—	11
8	6·2	45	45	3	41	1	25	7	13	30	—	14	1	30	—	2	9	4	9	—	—	6	9	—	—	6
														||												

Desiccator	Rel. Hum. %	28th day				35th day		39th day		43rd day		48th day		52nd day		134th day		202nd day	
		La		Ny		Ny		Ny		Ny		Ny		Ny		Ny		Ny	
		D	A	D	A	D	A	D	A	D	A	D	A	D	A	D	A	D	A
1	80	—	—	—	46	—	46	—	46	—	46	—	46	—	45†	2	43	4	41
2	70	—	—	1	46	3	44	3	44	4	43	5	42	5	42	24	23	36	11
3	60	1	—	1	44	1	44	1	44	1	44	1	44	1	44	12	33	43	2
4	50	1	—	2	45	2	45	2	45	2	45	2	45	2	45	29	18	47	—
5	30	7	—	—	33	—	33	1	32	1	32	1	32	2	31	33	—	—	—
6	20	9	—	—	20	2	18	2	18	3	17	3	17	5	15	20	—	—	—
7	10	12	—	—	11	3	8	3	8	4	7	5	6	5	6	11	—	—	—
8	6·2	9	—	—	6	—	6	—	6	—	6	—	6	1	5	6	—	—	—
		||																	

*=One dead, evidently damaged in handling on previous day.
†=One or more missing, having escaped from tube since previous count.
|| at foot of column=all remaining in this stage now dead. This column not repeated for subsequent days.
D at head of column=Dead.
A ,, ,, ,, =Alive.
La=Larvae.
Ny=Nymphs.

The desiccators were all kept in one incubator, the normal temperature fluctuation of which was 24·4°C. to 23·8°C., the maximum and minimum fluctuations being up to 25·5°C., once, and down to 20°C., also once only. The ticks were examined about twice a week, and detailed records were kept of the numbers dead and alive in each stage of development at each examination. There was often a doubt as to whether a tick was dead or alive. It was then recorded as doubtful, and carefully checked at the next examination. By this method it was always possible to decide what had been its correct status at the earlier count. The ticks were not fed at all during the period of the experiment.

Results.

Table III shows the numbers of the three stages, both dead and alive at the different humidities used, on the days when counts were made. The ticks that were recorded as doubtful have here been placed in the " dead " or " alive " columns by the method described above. This table shows that these ticks survive longest at high relative humidities. It will be seen that the ova and larvae are the stages least resistant to desiccation. At 30 per cent. relative humidity and lower there is a high mortality before the 1st nymph stage is reached, and this gets progressively higher as the humidity is lowered. The ticks that succeed in developing to the 1st nymph stage are much more resistant, and survive for a long period, even at the lowest humidity used, but a low humidity is still less favourable than a high one. It will be seen that the highest humidity used (80 per cent.) was by far the most favourable, and in view of the steady increase of longevity with humidity in this experiment it seems probable that a higher humidity would have been still more so. When the experiment was terminated on the 202nd day, the ticks that had been kept at 80 per cent. relative humidity were active and healthy, and showed no sign of having suffered from their long period of starvation.

TABLE IV.

Percentages of ova dying as ova, larvae, and developing to 1st nymph at each relative humidity used

Relative humidity per cent. ...	80	70	60	50	30	20	10	6·2
Percentage ova dying as ova... ...	0	0	2	2	21	37	55	67
Percentage ova dying as larvae ...	0	0	2	2	14	20	23	20
Percentage ova developing to 1st nymph	100	100	96	96	65	43	22	13

TABLE V.

Average period for development of survivors to larva and 1st nymph at each relative humidity used.

Relative humidity per cent. ...	80	70	60	50	30	20	10	6·2
Average period in days for development to larva	10	10	11	10	11	11	11	10
Average period in days for development to 1st nymph	17	17	17	17	18	18	18	18

Table IV shows the percentages (to the nearest whole number) of ova dying as ova, as larvae, and developing to the 1st nymph stage at the different relative humidities. It can be seen that down to 50 per cent. relative humidity practically all the ova developed to the 1st nymph stage. Below this there was a progressively increasing mortality in the earlier stages, but even at the extremely low humidity of 6·2 per cent., 13 per cent. of the ova developed to the 1st nymph stage.

Table V shows the rate of development to the different stages at the different relative humidities. As counts were made at 3 or 4 day intervals, and average differences of only one day appear in the table, it is impossible to say that these are significant. A detailed examination of the results (which are too voluminous to publish in full) suggests that if there had been an average difference of say two days or more in the rate of development it would have shown in this table. I think it is justifiable to say that it is extremely unlikely that the relative humidity affects the rate of development of the eggs of this tick.

Discussion.

This experiment is one of a series. It needs to be repeated at other, and particularly at higher temperatures, and with later stages of the tick as well. It would also be an advantage to extend the range of humidity up to saturation point. As, however, this work is unfortunately likely to be interrupted it was thought worth while to publish this result immediately, so as to draw attention to its disagreement with previous observations. Field observers all seem to have formed the opinion that this tick is favoured by low humidity. The only laboratory experiment I have been able to trace is that of Cunliffe (1921), described at the beginning of this paper. He found that a low humidity was the most favourable, but his conditions were not the same as in the present work. He started with 1st stage nymphs and fed them at intervals of about a month. He worked at a temperature of 30°C., and he adopted a different method of controlling his humidity. With regard to this last point, it is not clear from his paper whether his ticks were allowed to come in contact with the calcium chloride in the dry jar, or with water in the liquid state in the saturated jar, but it seems probable that in both cases they would be prevented from coming into actual contact. If in his wet jar the ticks were constantly in contact with water, it can well be understood that this would constitute an unfavourable environment for a land animal. It is more difficult to reconcile his other results—for " moist " and " dry " conditions—with the present ones. By sprinkling a few drops of water in the jar every day, obviously the ticks could only be in contact with water for a short period, if at all, and it seems unlikely that this would have a deleterious effect. It also seems unlikely that the higher temperature used would so completely alter the effect of a particular condition of the environment. It is more likely to cause a general shortening of the period of survival at all humidities. The only clue seems to be in the result he obtained under " dry " conditions. He says that 66 per cent. of his 1st stage nymphs under these conditions completed their metamorphosis. Now a 34 per cent. mortality between the 1st nymph and adult stages is extremely high for this tick, especially as he fed his at intervals much shorter than the period they can survive without food. Jobling found that " the nymphs are nearly all capable of development to the adult stage," and this observation has been fully confirmed in breeding the stock for this experiment. While there are no actual figures I can quote, I should estimate the mortality between the 1st nymph and adult stages at about 3 to 4 per cent.

This suggests that the mortality amongst Cunliffe's ticks was due to some cause other than the humidity at which they were kept.

With regard to the opinions expressed by Rodhain and Colas-Belcour, it seems probable that the microclimatic conditions of the normal habitat of this tick are very different from the conditions as measured in a meteorological screen. Williams (1923, 1924a, 1924b) found in the Egyptian desert that the relative humidity went up to a high value in the early morning, even in the dry season, and situations could always be found—in a cave, for instance—in which evaporation was low. From the figures he gives (1924a) of the percentage of moisture in the desert sand it seems probable in view of Buxton's work (referred to later) that the relative humidity in the sand air-spaces was fairly high. Kashkarov and Kurbatov (1930) obtained similar results in the Kara-kum desert. Buxton (1932) found in Palestine that the humidity, both relative and absolute, in cracks in walls and rocks was appreciably higher than outside, even at the driest time of year. The same author (1936) in studying the soils in which *Glossina submorsitans* and *tachinoides* pupate, found that in Nigeria, even under extreme conditions of heat and drought, the atmosphere in the soil spaces may be nearly saturated, even when the soil seems absolutely powder dry. Ot the two types of soil he tested, that from the thickets, containing a high percentage of humus, was in equilibrium with an atmosphere at 90 per cent. relative humidity when it only contained 4 per cent. of water, and it was shown to be a soil which had great water-holding power. The soil from the " woodland savannah " was almost pure sand, with very little water-holding power, and this was in equilibrium with an atmosphere at 90 per cent. relative humidity when it contained only 0·6 per cent. of water.

The facts quoted above appeared to offer an explanation of the apparent anomaly that there is a high mortality among puparia of *Glossina submorsitans* and *tachinoides* if they are kept in air which is far from saturation, while there is no evidence of such mortality in nature at the end of the dry season when the soil appears to be quite dry. It seems that a similar argument could equally well be applied to *Ornithodorus moubata*.

In the present experiments the longevity of the ticks is so uniformly graded from the low to the high humidity that it is extremely unlikely to be a false result due to other causes.

With regard to the present results, from Tables III and IV it can be seen that, although a high humidity is much the most favourable, yet a percentage of ova more than sufficient to carry on the race can develop to the 1st nymph stage even at very low humidities. Once they have reached this stage they are ready to feed, and in the wild state they can also, of course, move to a position with a more favourable microclimate. Even if they do not move, they are then capable of withstanding desiccation much better than in the earlier stages.

As mentioned previously, this experiment needs to be repeated at other, and particularly at higher temperatures, but it seems likely that the results of such repetitions would differ only in degree, and not in kind from the present ones. The general conclusion to be drawn seems to be that, though a high humidity (up to at least 80 per cent.) is more favourable to this tick than a low one, yet a proportion sufficient for the preservation of the species can survive even under very dry conditions, and no low humidity normally met with in nature is at all likely to be unfavourable enough to affect the numbers of a wild population.

Acknowledgments.

The ticks from which I bred my stock for this experiment were kindly supplied by Professor P. A. Buxton, of the London School of Hygiene and Tropical Medicine. I have to thank Mr. B. Jobling, of this laboratory, for much advice, particularly concerning the technique of handling these ticks.

Summary.

The longevity and development of the eggs of *Ornithodorus moubata*, Murray, at different relative humidities between 6·2 per cent. and 80 per cent. were investigated. It was found that :—

(1) All stages investigated, *i.e.*, egg, larva and 1st nymph, survived for a much longer period at high humidities than at low. The longevity showed a steady gradation through the range of humidities used.

(2) Even at very low humidities a sufficient proportion of eggs developed to the 1st nymph stage to carry on the race.

(3) The 1st nymph is much more resistant to desiccation than the earlier stages.

This result does not agree with opinions expressed as the result of field observations, or with the only previous laboratory experiment it was possible to trace. Reasons for both these disagreements are suggested.

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A NOTE ON THE FLY AREAS OF NORTH NYASA DISTRICT.

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Introduction.

In Nyasaland, as indeed in most territories in East Africa, the greatest single factor governing the distribution of both human population and stock is the presence of tsetse fly. Exact records, therefore, of the distribution of this fly are of importance. In the present article an attempt is made to summarise the present state of our knowledge regarding the prevalence of *Glossina* in the North Nyasa district.

In recent years, in that portion of the Lake Plain north of Karonga Boma, reported outbreaks of bovine trypanosomiasis (*T. congolense*) have increased and one suspected case of sleeping sickness was notified (1937). Owing, however, to the reported absence of tsetse fly certain ambiguities have arisen. The observations on which this report is based are the result of Veterinary Surveys made in the area during May–June 1937 and again in September 1938.

Probably the earliest records from this area were made by Dr. Meredith Sanderson (1911). As a result of a reconnaissance made in the Lake Plain and Songwe valley in June 1910 he reported that *Glossina fusca* (later identified as *G. brevipalpis*) was common on all the river-banks north of Karonga. The southern limit seemed to be the banks of the N. Rukuru River, while stretching northwards, fly were abundant up to the Songwe River and westwards along the Songwe valley as far Maheye River (Map, fig. 1). Dr. W. A. Lamborn (Dept. Record 1919) reported *G. brevipalpis* to be present north of Karonga and also *G. morsitans* in considerable numbers along the N. Rukuru River. Later observations by Veterinary Stock Inspectors and native "fly boys" were negative. Potts (1937) refers to this fly-belt, and Swynnerton in a footnote to the same article states that *Glossina brevipalpis* occurs in Nyasaland.

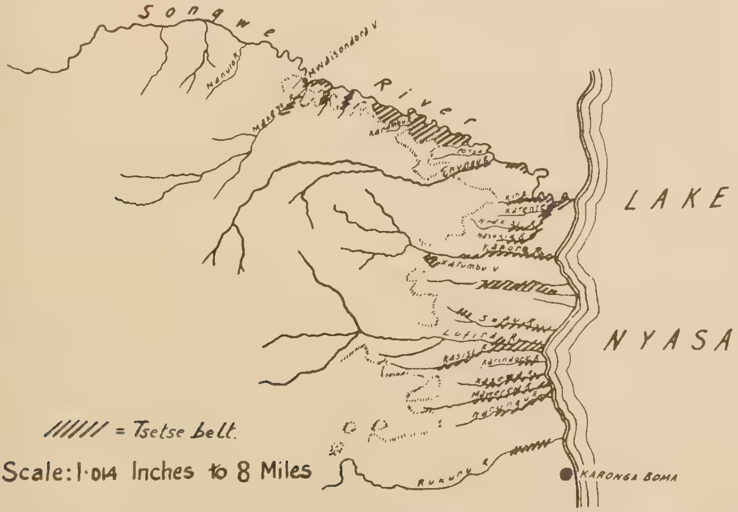

Fig. 1. Map of North Nyasa by Dr. Meredith Sanderson (Bull. Ent. Res., 1911) showing distribution of tsetse flies at that time.

General Description of Physiography of Area.

The North Nyasa district, as a whole, is very mountainous and varies in elevation between 1,500 ft. and 8,000 ft. above sea-level. The area with which this article is chiefly concerned lies in the northern half of the district, the southern limit being the Stephenson Road. The remaining boundaries are Lake Nyasa on the east, the Songwe River on the north, and the N. Rhodesia-Nyasaland watershed on the west.

The presence of tsetse fly in the area of North Nyasa south of the Stephenson Road has never even been suspected.

For brevity of description this northern area may be broadly divided into four regions.

(1) Lake Plain—having an average altitude of about 1,800 ft. above sea-level.

(2) Foot-hills—separating the main Masuku Massif from the Lake Plain. They represent a plateau deeply dissected by numerous rivers and falling in most places in gentle slopes to the Plain.

(3) Masuku Highlands.

(4) Nyondo Plateau.

Regions (1) and (2) alone afford conditions favourable for the existence of tsetse.

Vegetation.

The soils on the Lake Plain are all alluvial and suitable for cotton cultivation. On the best agricultural lands on the Rukuru River and around Karongo *Acacia albida*, *Kigelia aethiopica* and *Trichilia emetica* dominate, while further north around Kapora and the lower reaches of the Songwe, *Combretum–Acacia–Terminalia* associations are found. Other species occurring are *Bauhinia thonningii*, *Zizyphus jujuba* (common), *Annona* sp., *Vangueria tomentosa*, *Ficus* sp., and palms (*Hyphaene crinita*), with occasional baobab trees. Throughout these types grass is long and is fiercely burnt. Bananas form a staple food for the native inhabitants, and around native villages, especially near the Songwe, dense banana groves, supported by mango and *Cassia* trees, are found.

The forests along the foot-hills offer such a changing variety as prevents a comprehensive description of their composition. In areas where the density of native population is low or where cotton cultivation has not been adopted, the river-banks carry a dense primary growth of shrubs and creepers. Flourishing banana groves around villages increase the jungle effect. On the immediate hill slopes *Sterculia* sp. and *Afzelia* sp. are the principal dominants. Other species which occur are *Terminalia hildebrandtii*, *Bauhinia thonningii*, *Pseudolachnostylis maprouneifolia*, *Sclerocarya caffra*, *Burkea africana*, etc. At the higher altitudes (above 2,000 ft.) *Brachystegia–Isoberlinia–Diplorrhynchus* associations predominate, with pockets of *Uapaca kirkiana* where soil conditions are suitable.

Limits of present Fly-belt and Species of Tsetse concerned.

The present distribution of tsetse fly during the dry season (April to December) in the North Nyasa district can best be visualised by reference to the Map (fig. 2). Here fly is seen to be present only along the foot-hills bounding the Lake Plain on the west and also along the Songwe valley from the Chungu River to the Nantakwa River. It can best be described as a narrow continuous belt of tsetse lurking in the defiles of the foot-hills from Katumbe village in the south, around the Yembe Hills and along the Songwe valley as far west as the Nantakwa River.

Glossina brevipalpis was the only species of *Glossina* encountered. The habits of this fly make its detection difficult as " Shunning the bright light of the open savannah, (it) lurks during the day in the recesses of its thicket homes" (Potts), feeding only at dusk or after dark. It is probably for this reason that our records of this fly-belt are so scanty. *G. brevipalpis* seems to have existed for years near villages in the Songwe without even the natives being aware of its presence. Debility and death amongst their cattle due to *Trypanosoma congolense* were explained as being due to "poison" in the waters of certain rivers, notably Chungu River, and certain grazing grounds near the hills were "evil."

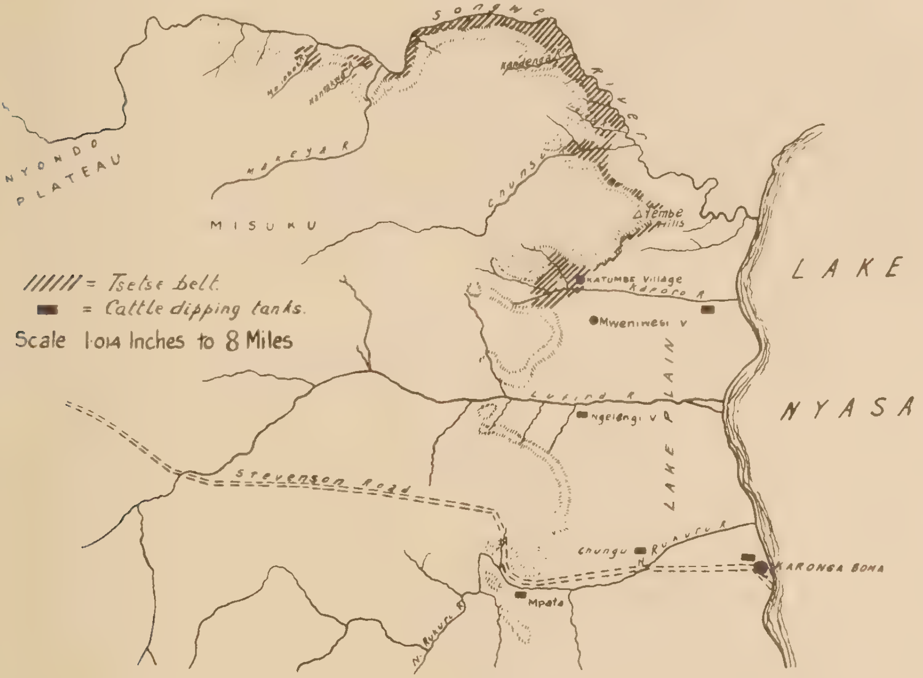
SONGWE RIVER
NYONDO PLATEAU
MBEYA R
MISUKU
CHUNSU
Kandenga
Yembe Hills
KATUMBE Village
Kaporo R
Mweniwesi V
LAKE
NYASA
LAKE PLAIN
Lufira R
Ngelengi V
Stevenson Road
Chungu
RUKURU R
KARONGA BOMA
Mpata
N. RUKURU R
////// = Tsetse belt.
▬ = Cattle dipping tanks.
Scale 1·014 Inches to 8 Miles

Fig. 2. Map of North Nyasa showing present distribution of tsetse flies.

The present absence of tsetse from the Lake Plain has resulted from a combination of several factors. Intense cultivation of river-banks for the growth of native crops (cotton and rice), the increase of the cattle population to the point of overstocking, and grass burning, have all combined to produce vegetative conditions inimical to *G. brevipalpis*. The fly area along the Songwe River is almost entirely uninhabited west of Chungu River, while the soils on the foot-hills at Yembe and to a lesser extent at Katumbe are unsuitable for cotton cultivation. This "clearing" effect of native cultivation has possibly been intensified owing to the continuous nature of the cropping system, rice being grown in the wet season, and cotton during the dry months of the year. A glance at the cattle concentration map prepared of this Lake Plain area is sufficient to emphasize the absence of tsetse.

Present Fly Density.

A preliminary survey of the vegetation of this area (assisted by a map showing the cattle concentration and epidemiology of recent trypanosome outbreaks) points to certain areas where the main densities of *G. brevipalpis* might be expected. The banana groves and primary fringing forests along the banks of rivers pouring into the Songwe west of Chungu Hill, as well as the *Brachystegia* forests of Yembe and

Katumbe Hills, alone afford the necessary shade conditions. In other areas where conditions have been altered either by cultivation or by large scale clearing for village sites, the fly has receded. Further, the density of the fly within the fly-belt has definitely decreased as compared with earlier descriptions. Even after search, prolonged several hours after dark in banana groves, along native paths and along river beds, at most two specimens were captured in one day, and on many days the results were entirely negative. Baboons, game, and in some places cattle afford abundant food supply.

Regarding the possible spread of fly during the wet season beyond the limits of the fly-belt as defined above, natives definitely state that biting flies are more common during the rains. But this evidence is unreliable with regard to tsetse fly as this prevalence of biting flies coincides with the seasonal presence of *Haematopota mactans*. The only definite observations made were at Katumbe village. Here prolonged search during the dry season was unsuccessful, and the only specimens obtained were sent in by natives during the rains in February, at which time fly was reported to be fairly prevalent. The dependence of this fly on deep shade would render its spread in the wet season very limited, but native evidence supports the assumption that density does increase within the fly-belt with increased humidity.

Acknowledgments.

I am greatly indebted to the late Mr. B. D. Burtt, Department of Tsetse Research, Tanganyika, for the generous way in which he placed his unique knowledge of Survey Botany at my disposal during his visit to Nyasaland in 1936.

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THE ECOLOGY OF THE PUPARIUM OF *GLOSSINA* IN NORTHERN NIGERIA.

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(Plates VII–IX.)

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Introduction.

In the past, much study has been devoted to the seasonal fluctuations in the size of adult tsetse populations in relation to climate (Nash, 1930, 1933 and 1937; Lloyd, 1935; Jackson, 1937). No similar study has ever been made upon pupal density and mortality in relation to the microclimatic conditions in the breeding-grounds. Further, all estimates of seasonal pupal mortality have been based on collections of puparia made at different times of year and brought into the laboratory to await emergence. The climate in the laboratory is so entirely different from that of the soil in the breeding-ground, that these results may have little bearing upon what really happens under natural conditions.

The basic data for this paper were collected from the plain of the Katagum River near Gadau in Northern Nigeria (12°N., 10°E.); only *Glossina morsitans* and *tachinoides* occur in this fly-belt. For a description of the climate, vegetation, and general tsetse ecology of this district the reader is referred to " Climate, the Vital Factor in the Ecology of *Glossina* " (Nash, 1937).

The earlier workers at Gadau failed to find puparia in the rains, and their final conclusions were that " the breeding of *G. morsitans* and *G. tachinoides* in Northern Nigeria is largely confined to the dry season " (Taylor, 1932). When the writer found that the adult population of *G. morsitans* and *G. tachinoides* becomes greatest in the rains, he concluded that the early investigators had probably underestimated the extent of the wet season breeding. It was not until the middle of 1937 that he first discovered the sites utilised by the females in the rains.

Types of Breeding-ground.

The breeding-places used by the pregnant females vary according to the time of year, and may be divided into the five following types :—

" *Residual Forest Islands.*"—The only surviving remnants of the original forests of this part of the country persist as small islands of partly evergreen trees, with crowns united by creepers to form a high shade canopy. These clearly defined islands are composed of true forest species cemented into a whole by peripheral and intrusive thicket which protects the islands from wind and fire. There are four such islands in the 16 square miles of fly-belt under investigation ; they are some 500 yards long by 50 to a 100 yards wide, and only occur on the banks of drainage depressions in the river-plain. Puparia are found in the rich humus of the forest floor throughout the dry season (Plate VII, fig. 1, and Bull. Ent. Res. **28,** Pl. V, fig. 1).

" *Small Thickets.*"—Hundreds of small isolated thickets occur in the heavy woodland savannah of the river-plain. They consist of several large trees overgrown with creepers, and may be regarded as minute residual forest islands ; however, owing to their very small size, their protection from radiation and wind is far less complete. Puparia are found in the humus of the thicket floors throughout the early and mid-dry seasons (Plate VII, fig. 2).

" *Margin of the River-bed.*"—In many stretches the banks of the Katagum River are fringed with a species of willow (*Salix*) which overhangs the margin of the river-bed, forming a long line of shrubbery ; dense low shade is cast, and the sand, though dry on the surface, is moist at a depth of 3 inches. The river margin breeding-ground only becomes available when the river ceases to flow at the commencement of the very hot weather ; two and a half months later the river comes down in flood and the site is destroyed.

" *Logs.*"—Puparia are found in the rains under fallen trees in the open woodland savannah (Plate IX, fig. 2).

" *Seedling Palms.*"—During the rains puparia are also found throughout the open woodland savannah beneath the fronds of the young Dum palm (*Hyphaene thebaica*) (Plate IX, fig. 1) ; seedlings of this species grow in clumps, some four feet high and bristling with fan-shaped leaves which almost touch the ground. Each leaf may be compared to a hand with the fingers extended and separated ; each leaflet is V-shaped in cross section, so that the rain pours down these miniature gutters, being deposited around the periphery of the clump and leaving dry patches of soil beneath the base of each leaf. Breeding takes place in these patches of drier soil.

Having discovered the main breeding-grounds, the last two years were spent in making a detailed study of them.

Methods employed in the Investigation.

Seven breeding-grounds, including three different residual forest islands, were selected for an intensive investigation, and the following technique was devised in an attempt to observe the time of year when each breeding-ground was first occupied and finally evacuated, the same two consecutive dates in each month were allocated to the searching of each breeding-ground ; thus " Logs " were invariably visited on the 22nd and 23rd of each month, even if it was a foregone conclusion that nothing would be found. On each of the two consecutive days, four supervised searchers spent four hours in the breeding-ground. Thus at monthly intervals 32 boy-hours were spent on each breeding-ground.

In order to study seasonal pupal mortality under natural conditions, shallow rectangular boxes were constructed, $2\frac{1}{2} \times 9\frac{1}{2} \times 1\frac{1}{2}$ inches in depth. The top and bottom of each box was made of fine-meshed copper netting attached to a framework of seasoned mahogany. At one extremity of the box, a hole, half an inch in diameter, was bored through the top and was fitted with four inches of glass tubing of similar diameter ; the tube just protruded through the lid into the interior of the box, the floor of which was lined with a thin layer of soil. The box was buried at $1\frac{1}{2}$ inches depth in a typical part of the breeding-ground, with the glass tube projecting above the surface and closed with a cork. At the end of each days' searching in a breeding-ground, the puparia were counted and were then poured down the tube on to the thin layer of soil that lined the bottom of this underground chamber ; the cork was rapidly replaced in the mouth of the tube, and the neck sealed with wax. Apart from its use as a means of introducing puparia into the underground cell without disturbing the soil, the light from the top of the glass tube attracted the hatching flies, so that the tube acted as an inspection window which enabled the observer to know when emergence was complete and it was safe to dig up the box. By daily observation it was found possible to record the date of the last emergence, and thus to get a conservative estimate of the normal duration of the pupal period, based on the assumption that providing the sample is large, the last puparium to hatch must have been very young at the time of collection. Ten days after the last emergence the box was dug up and brought to the laboratory where the dead puparia were counted.

The shallowness of the box and the permeability of the material forming its top and bottom assured that the puparia experienced the natural seasonal conditions of soil atmospheric humidity and temperature.

The puparia removed from a breeding-ground were invariably replaced with a similar number collected from the bush on the far side of the river ; thus the local populations should not have been reduced in size by the monthly searches.

The following microclimatic factors were measured by instruments kept in the immediate vicinity of the buried box : maximum soil surface temperature, maximum temperature at $1\frac{1}{2}$ inches depth (read every other day), and monthly evaporation at 5 inches above the surface as recorded by a white Livingston atmometer bulb. In addition the soil water content of each breeding-ground was measured on the fifteenth day of each month from a soil sample of about 30 grams taken at $1\frac{1}{2}$ inches depth. The samples were taken at dawn and were brought to the laboratory in air-tight bottles packed in cotton wool ; immediately on arrival samples were weighed, heated to constant weight in an oven at 105°C., and then re-weighed. The water content was expressed as a percentage of dry weight.

The soil surface maximum temperature readings proved valueless, as they fluctuated violently from day to day depending upon whether or not the leaves in the high canopy cast a shadow over the bulb. Since any effect caused by the passage of a beam of sun over the buried box would be recorded by the thermometer at $1\frac{1}{2}$ inches depth, and since the adult is always free to avoid the sun by moving into shadow, such transitory records of sun temperatures are obviously irrelevant. Surface shade maxima, from readings taken in Stevenson screens on the ground, would have been useful as recording a factor that probably influences the parent at the time she evacuates the breeding-ground.

Soil minimum temperatures should also have been recorded in addition to maximum, as from the two sets of readings an approximation of the mean temperature could have been obtained.

Having been unable to afford the time or the instruments needed for more than one set of observations from each breeding-ground, the writer has laid himself open to the criticism that he is assuming that soil conditions are uniform in a breeding-ground. The assumption is probably fairly safe, except in May when the first storms break ; at this season a sampling experiment showed considerable variations in soil water content due to the screening effect of vegetation, but once the rains really break, the soil in a small area becomes uniformly wet.

Dr. R. Harding kindly carried out for the writer a soil temperature sampling experiment in each breeding-ground. He found that the soil temperature in the official station did not vary by more than 1·5°F. from the mean of six other readings taken simultaneously in different parts of the same breeding-ground. There was one exception, namely the Log station which was 5°F. hotter than the mean for six other logs.

The methods used have evident limitations, but they indicate that certain factors have little relation to pupal mortality, and that others are important. We can, moreover, begin to perceive the limits within which such factors as soil temperature are favourable or the reverse. In a word, one begins to measure the environment's effect on the puparium.

Description of each of the Seven Stations selected.

1. *The Control Forest Island.*—This residual forest island is the coolest and dampest in the area, being well protected by thicket (Bull. Ent. Res. **28,** Pl. V, fig. 1).

2. *The Experimental Forest Island.*—Originally the climate in this island was very similar to that in the Control, but in October 1937 it was made the object of an experiment in partial clearing, all the peripheral and intrusive thicket wind-break being removed. The effect upon pupal density and mortality of a set of microclimatic conditions which are abnormally severe for a residual forest island have given very interesting results.

3. *Taylor's Forest Island.*—This forest island can be used for a longer period than any of the others because of the range of conditions which it affords. In places, owing to the absence of peripheral thicket, tongues of true forest extend to the island's margin ; these strips support very little low vegetation, and dry up so rapidly after the rains that they can be used at once for breeding (Plate VIII, fig. 1). The instrument station was situated in one of the tongues of true forest (Plate VIII, fig. 2). In other parts one finds dense undergrowth, high shade, and a peripheral thicket wind-break ; here puparia may be found even in the very hot season. Taylor's Forest Island was the area in which Buxton and Lewis kept their screens 1, 2 and 4, and of which they made a small map (1934, p. 223).

4. *Small Thickets.*—Two adjacent small thickets, typical of the hundreds that exist in the open woodland, were selected. Microclimatic conditions were investigated in one only, the puparia collected from the floor of both thickets being buried beside the instruments (Plate VII, fig. 2).

5.—*Under Palm Fronds.*—Puparia were collected from under the palm fronds throughout an area of heavy woodland savannah in which the palm (*Hyphaene thebaica*) is a dominant (Plate IX, fig. 1). All puparia collected in the area were buried beside the instruments under one typical clump of seedling palms.

6. *Under Logs.*—Puparia were searched for under all the fallen trees that occur in the same area of heavy woodland savannah, and were buried under one typical log (Plate IX, fig. 2).

7. *Margin of River-bed.*—Puparia collected along the margin of the river-bed were buried beside the instruments, which are situated at a spot chosen as being representative.

The last five breeding-grounds are in the vicinity of Taylor's Forest Island, whereas the Control and Experimental Islands are situated some three miles further up the river-plain.

TABLE I.

Mechanical Analyses and certain Constants determined for Soil Samples from the seven Breeding-grounds investigated.

Mechanical Analyses (oven-dry, unignited basis)	Control Forest Isl.	Expt. Forest Isl.	Small Thicket	Taylor's Forest Isl.	Log	Palm	River-bed
Coarse sand	4·2	2·9	9·5	0·7	10·7	2·3	97·8
Fine sand	37·5	57·6	45·8	70·6	38·9	80·5	2·1
Silt	16·7	10·0	13·3	8·2	21·0	4·5	0·0
Clay	25·4	18·7	25·7	18·0	25·4	12·9	0·0
Hygroscopic moisture	5·7	4·1	3·6	2·3	3·0	1·0	0·1
Calcium carbonate	0·0	0·0	0·0	0·0	1·4	0·0	0·0
Loss on ignition	17·7	12·9	7·8	7·0	6·8	3·1	0·3
Organic matter (c×1·724)	15·5	11·2	5·5	8·5	2·9	1·6	0·0
pH	6·4	7·0	7·6	7·8	8·1	7·6	*(7·0)
Max. water-holding capacity	81·4	69·6	53·9	50·7	42·2	37·5	21·2
Water content at sticky point	55·9	51·6	34·1	31·1	30·9	25·1	*(6·6)
Moisture equivalent	35·8	27·6	29·4	20·0	26·5	13·0	2·2

* The pH and sticky point figures are without significance for the River-bed sample, which consists of coarse sand, containing no colloidal matter.

ENVIRONMENTAL CONDITIONS.

Soils of the Seven Stations.

Samples of soil, taken at 1½ inches depth from the vicinity of each station, were brought to England for examination.

The writer found the maximum water-holding capacity figure for each soil himself, but for the moisture equivalents he is indebted to Dr. Keen of Rothamstead, and for the mechanical analyses and other constants to Professor G. W. Robinson of the University College of North Wales.

Mechanical Analyses.—An examination of the figures given in Table I shows that the female tsetse is not particular in her choice of soils, which range from the fairly heavy clay of the Control Forest Island, through a series of heavy loams and the fine sandy loam of the Palm station, to the coarse sand of the River-bed; organic matter may be abundant, as in the first station, or absent, as in the last. The range is so wide that the type of soil cannot in itself be a factor in the selection of breeding-grounds.

Loss on Ignition and Organic Matter.—Since carbonates are virtually absent the loss on ignition may be taken as consisting of organic matter + water combined in clay. As would be expected, organic matter is abundant in the forest islands and small thickets, much less under palms and logs in the open woodland, and absent from the coarse sand of the River-bed.

pH Values.—With the exception of the Control and Experimental Forest Islands, all soils are slightly alkaline.

Maximum Water-holding Capacity.—To find this constant for each soil an experiment was suggested by Dr. C. G. Johnson which would simulate a rising water-table : about 100 grams of soil were poured little by little, and with some tapping, into a filter-paper within a 4½ inch diameter funnel. The funnel was lowered into a jar of water until the soil in the apex was just wetted, enabling the whole to absorb moisture from below. When the soil had become visibly wet the height of the water in the jar was gradually raised, until after 18 hours it was level with the soil surface. After a further 48 hours the funnel was removed and left to drain for 4 hours, the mouth being covered with a wet filter-paper to prevent evaporation. The saturated soil and filter-paper (for which a correction was made) were then weighed and afterwards heated to constant weight at 105°C. The water content of the saturated soil was expressed as a percentage of dry weight, and was taken as representing the maximum water-holding capacity of that soil. The experiment was repeated for three of the soils, giving results that were within 2 per cent. of those found on the first occasion.

Reference to Table I shows that there are great differences between the maximum water-holding capacities of the different soils, the capacity being greatest in the forest islands and small thickets. Soils in several of the breeding-grounds were extremely close to saturation under the climatic conditions which prevailed in August and September 1938 (see Table III).

The *Sticky Point* measures the maximal imbibitional capacity of the soil colloids for water, together with water held in the interstices. The sticky point is the water content at which the attractive power of a soil for water is *just* satisfied, whereas the maximum water-holding capacity (as measured by the writer) is the maximum water content that a saturated soil can hold against gravity. Reference to Table III shows that in the floods of September 1938 the soil water content rose above the sticky point in every station.

The sticky point moisture content shows a good correlation with loss on ignition, and also a good relationship with the maximum water-holding capacity (*vide* Table I). The soil from the Control Forest Island gives the greatest value for each of these three constants, and the sand from the River-bed the least.

The *Moisture Equivalent* is a measure of the retentiveness of a soil for water under a given centrifugal force, or roughly colloid water less interstitial water. The figures given in Table I represent the weight of water held per 100 grams of oven-dry soil against a force of 1,000 g.

The poor water-retaining powers of the soil from Taylor's Forest Island and the Palm stations account for the very low water contents recorded from these sites in the dry season (see Table III), whilst the high moisture equivalent of the Control explains the relatively high water contents recorded there in the very hot weather (March and April).

TABLE II.

Mean Monthly Maximum Soil Temperature at 1½ inches Depth (1937–1938).

Months	xi	xii	i	ii	iii	iv	v	vi	vii	viii	ix	x	Average
River-bed	—	—	—	—	75·6	88·0	—	—	—	—	—	—	—
Control For. Is. ...	80·4	78·1	77·7	81·3	86·2	91·8	88·9	84·2	77·2	75·7	77·7	79·5	81·6°F.
Taylor's For. Is. ...	82·0	80·6	78·3	81·7	85·1	92·3	90·7	85·3	79·3	77·0	78·8	79·9	82·6°F.
Expt. For. Is. ...	86·4	82·4	81·3	88·7	91·0	97·2	90·7	86·2	78·8	77·9	80·8	83·1	85·4°F.
Small thickets ...	87·6	85·8	85·6	89·2	93·0	98·0	95·1	87·1	78·4	79·3	80·0	79·7	86·7°F.
Palm	84·7	81·5	79·5	86·5	93·9	104·9	97·9	88·9	81·5	79·7	81·3	83·1	87·0°F.
Log	93·0	96·3	92·3	98·4	102·3	108·3	100·9	90·9	81·9	80·6	78·8	86·0	92·5°F.

TABLE III.

Soil Water Content at 1½ inches depth on 15th day of each Month, expressed as a Percentage of Dry Weight (1937–1938).

Months	xi	xii	i	ii	iii	iv	v	vi	vii	viii	ix	x	Average
River-bed	—	—	—	—	5·8	3·5	—	—	—	—	—	—	—
Control Forest Island ...	9·0	9·4	8·7	9·6	7·6	6·4	20·4	11·2	41·7	50·9	57·9	21·4	21·2
Expt. Forest Island ...	6·6	4·4	4·9	5·0	5·1	4·0	20·2	7·2	31·9	51·0	60·8	49·5	20·9
Small thickets	6·0	6·3	5·4	6·5	5·5	4·3	12·0	6·1	31·5	48·2	52·2	36·5	18·4
Taylor's Forest Island	3·7	3·1	3·2	3·6	2·9	2·9	6·4	9·8	24·1	35·5	41·2	12·4	12·4
Log	2·9	3·0	2·6	3·0	2·3	2·0	2·8	4·6	23·7	32·9	40·1	16·5	11·4
Palm	1·6	1·6	1·4	1·4	1·4	1·4	4·1	2·2	20·5	27·8	35·7	9·9	9·1

TABLE IV.

Mean Monthly Evaporation (*in cc.*) *at* 5 *inches above Soil Surface* (1937–1938), *measured by Livingston White Spherical Atmometers.*

Months	xi	xii	i	ii	iii	iv	v	vi	vii	viii	ix	x	Average
River-bed	—	—	—	—	30	38	—	—	—	—	—	—	—
Palm	27	27	29	40	55	56	33	22	7	2	6	13	26·4
Taylor's Forest Island ...	29	30	35	42	52	51	30	21	7	2	5	14	26·5
Control Forest Island ...	31	32	35	42	55	54	31	24	8	2	5	16	27·9
Small Thickets	29	33	40	45	56	55	35	25	10	5	7	16	29·7
Expt. Forest Isl. ...	35	35	38	45	58	57	37	27	11	4	8	20	31·2
Log	36	37	41	53	70	70	50	36	12	5	7	17	36·2

The Microclimates of the Seven Stations.

Owing to the absence of continuous climatic records of the pupal environment, a year's data for the seven stations are given in Tables II to IV. They indicate the range of conditions occurring in the field, though not necessarily the conditions under which puparia are always found. As will be shown later, in some months when the climate of a breeding-ground becomes too severe the females will desert it in favour of another where more equable conditions prevail ; this evacuation coincides with an increase in the mortality of the last batch of puparia found.

The data shown for the Experimental Forest Island refer to a period *after* the completion of the partial clearing.

Features of the year dealt with in the Tables were an abnormally warm cold season, and a wet season in which the river-plain was flooded in early September—an event that only takes place every two or three years.

Mean Monthly Maximum Temperature.

Reference to Table II shows that the Small Thicket, Palm and Log stations are the hottest ; puparia cannot be found in these breeding-grounds during the very hot weather. Note how much cooler is the River-bed station, where pupal mortality in the hot season is much lower than elsewhere. Buxton & Lewis (1934) showed that a temperature of 98·6°F. (37°C.) kills puparia in a few days, and that the mortality among puparia kept at a constant temperature of 86°F. (30°F.) is higher than at 75°F. (24°C.), even at the most favourable humidity. In East Africa, Potts (1933) found that *G. morsitans* puparia failed to survive 13 days exposure to a constant temperature of 95°F. (35°C.). These results suggest that in those sites where the mean monthly maxima are over, say 95°F., the conditions are likely to be unsuitably warm.

Throughout the dry season (November to May) the temperature varies greatly from station to station, but in the rains (June to September) the differences are very small, suggesting that temperature in the wet season is unlikely to be the causal factor of variations in pupal mortality or the type of breeding-ground selected.

As stated above, the cold season for the year given in the Tables was unusually mild, but in the colder January of 1937 the Control and Experimental Forest Islands gave mean monthly maxima of 71·2° and 71·4°F. respectively, with a mean pupal period of 55 days. Buxton & Lewis (1934) showed that at the constant temperature of 75°F. the pupal period of *G. morsitans* was 33 days ; thus a pupal period of 55 days in the field denotes a much lower mean temperature, possibly about 65°F. If the atmosphere in the soil is not saturated, such low temperatures may be the cause of the high pupal mortalities observed in the field in January 1937 ; the prolongation of the pupal period causes abnormal loss of weight (Buxton & Lewis, 1934, p. 220).

Buxton & Lewis (1934) suggested 75°F. (24°C.) as the optimum constant temperature for the puparium. A study of the maximum temperatures recorded in the field suggest that in the cold season the temperature may fall too low, and that in the hot season it may rise too high, whereas in the rains it is probably a factor of minor importance.

Absolute Maximum Temperatures.

Absolute maxima of 111·2°F. were recorded from both the Palm and Log stations, at a time when no puparia were being found, as these sites had already been evacuated. In the other stations the absolute maxima never approached the upper fatal limit for puparia.

Soil Water Content.

Examination of Table III shows that the Control Forest Island as well as being the coolest station is also the wettest, whereas the Palm and Log Stations are the driest as well as being the hottest.

Buxton & Lewis's results (1934) suggest that pupal mortality is only low if the atmosphere is nearly saturated. Buxton (1936) published a curve showing that the atmosphere in a sample of forest island soil (he called it " thicket ") would not be saturated if the water content fell below about 4·8 per cent., or below about 0·8 per cent. if the soil came from the sand ridges. The physical properties of Buxton's so called " thicket " soil are similar in all respects to those shown for the Experimental Forest Island in Table I ; his sand ridge soil would come in between the Palm and River-bed stations in this Table.

Reference to the monthly water contents shown in Table III, and to Buxton's curve referred to above, suggests that the soil atmosphere in the Control Forest Island and River-bed was always saturated, whereas in the Experimental Island and Small Thicket it was probably saturated except in April. In the fringe of Taylor's Forest Island, the Log and Palm stations, the soil atmosphere was probably unsaturated throughout the dry season.

The effect of partially clearing the Experimental Forest Island has been to make it one of the wettest sites in the rains.

Reference to the maximum water-holding capacities of the different soils given in Table I will show that in September many of the stations must have been nearly water-logged. Nash (1933) and Buxton & Lewis (1934) showed that puparia cannot survive in water-logged soil, but unfortunately no laboratory work has yet been done upon the effect upon pupal mortality of soils approaching saturation.

It should be noticed that during the rains there is a very considerable difference in the soil water content figures for the various stations, suggesting that, unlike temperature, it may be a factor related to variations in pupal mortality or the type of breeding-ground selected.

Evaporation.

Apart from the much lower evaporation occurring above the wet sand in the river-bed, it will be observed from Table IV that there is remarkably little variation in the evaporation in the different stations, suggesting that evaporation at 5 inches cannot have much relationship to the seasonal shifting of the breeding-grounds.

At the only two stations where evaporation was also measured at four feet, the following interesting results were observed: In the dry season the daily evaporation in the Experimental Island was always about 3 cc. greater at 4 feet than at 5 inches, but in the Control it was always about 4 cc. *lower* than at 5 inches. This suggests that in the normal forest island a current of air probably penetrates the wooded stems of the surrounding thicket near ground-level, and, blowing across the forest floor, causes high evaporation at the soil surface; but at a greater height the thicket is leafy and forms an effective wind-break, resulting in a lower evaporation at the higher level. The ameliorative effect exerted by peripheral thicket upon the climate within a forest island is much greater some feet above ground-level; thus for the whole dry season the mean daily evaporation at 5 inches in the Control was only 4 cc. lower than in the Experimental Forest Island, but at 4 feet it was 11 cc. lower. These results suggest that had evaporation been measured in all stations at 4 feet instead of 5 inches much greater differences would have been observed, and possibly a relationship established between this factor and the evacuation of the breeding-grounds by the adults.

SEASONAL SHIFTING OF BREEDING-GROUNDS.

In figs. 1 and 2 the seasonal pupal density (expressed as puparia per boy-day) is shown for each of the seven breeding-grounds over a period of two years.

The data have been plotted on a logarithmic scale so as to indicate the rate of increase or decrease in density, and to give the low readings full expression at the expense of the high. This is desirable because a rise in density from 5 to 10 puparia denotes a 100 per cent. increase in the pupal population, and is therefore biologically more important than a rise from 200 to 220 puparia which denotes only a 10 per cent. increase; yet if actual increase instead of rate of increase was plotted, this latter rise would be given four times the value of the former, because the actual number of puparia involved is four times greater. Since a logarithmic scale has been used it follows that if two curves on the graph run parallel with each other, they must denote identical rates of increase. On the scale employed a 25 per cent. increase in density will correspond to a curve rising at an angle of 20°, 50 per cent. at 35°, 100 per cent. at 50°, 200 per cent. at 61°, 500 per cent. at 71·5° and 1,000 per cent. at 76°.

Very low pupal densities ranging from 1·0 down to 0·1 P.B.D. cannot be plotted on this scale because the logarithm of 1 is 0; however, periods when the pupal density was less than 1 are indicated on the graph by a horizontal line ruled just above the abscissa.

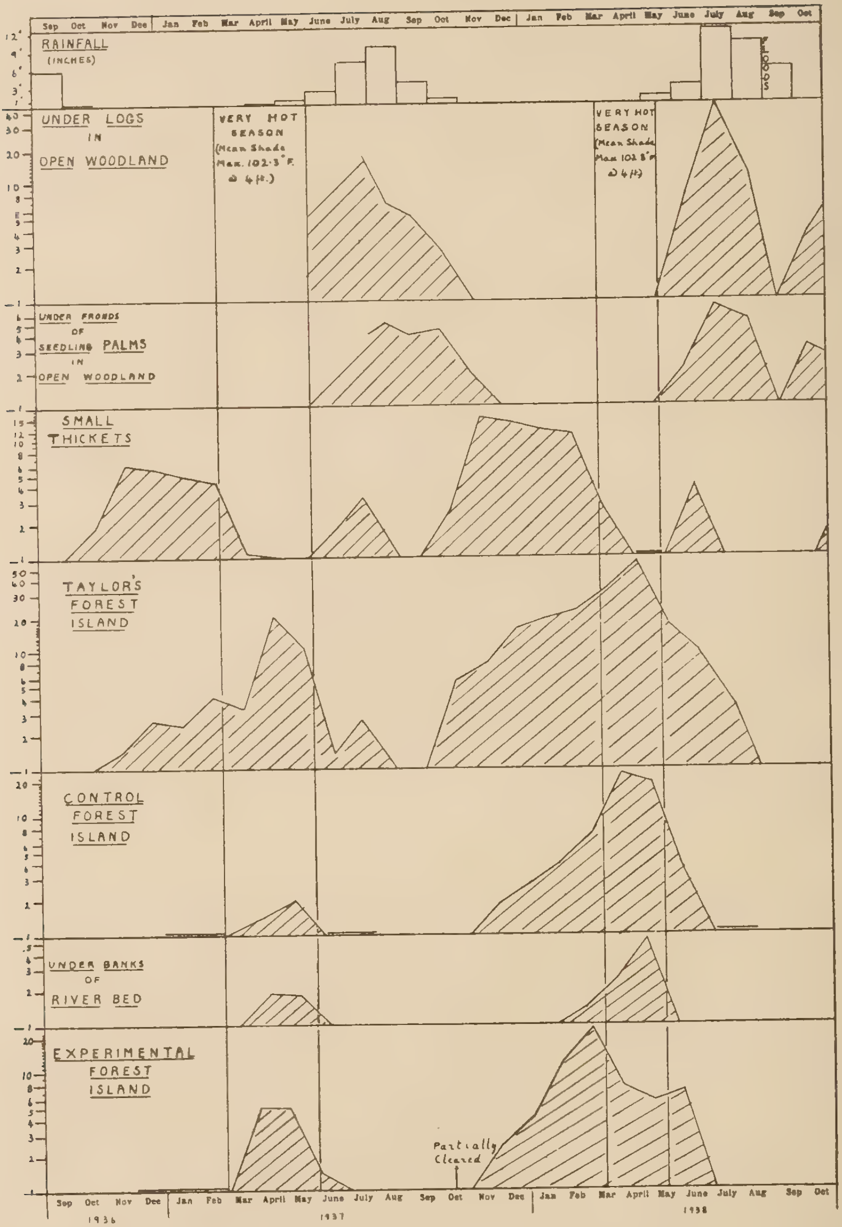

Fig. 1. The seasonal shifting of the breeding-grounds of *G. morsitans* at Gadau, N. Nigeria. (Pupal density expressed as puparia per boy-day of 4 hours, plotted on a logarithmic scale.)

Glossina morsitans (fig. 1).

Under Logs and Palm Leaves in Open Woodland Savannah.

Unfortunately these two types of breeding-ground were not discovered until the middle of 1937. Logs and palms are used throughout the rains when all other sites become too wet and are evacuated. Owing to rising temperature in the early dry season these breeding-grounds soon become unfavourable, and are not used again until the following rains. Note how in September 1938 when there were floods, even these sites became too wet and were deserted for a month.

Small Thickets in Open Woodland Savannah.

In the early dry season (October and November) breeding shifts from the Logs and Palms to the greater shelter of the Small Thickets, but they in turn become too hot in March and are not used again until the early rains ; by July or August the Small Thickets have become too wet and are evacuated in favour of the Logs and Palms. Note how perfectly this cycle repeats itself throughout the two years, even the rate of increase and decrease in pupal density being very similar with the repetition of seasons.

Taylor's Forest Island.

As described on p. 262, owing to the variations in the density of the vegetation, the pregnant female can find sites in this forest island which will satisfy her requirements at all seasons except the heavy rains. With the evacuation of the Small Thickets in the very hot weather, pupal density becomes maximal in Taylor's Forest Island, but the puparia are only found in the densest parts and no longer in the tongues of true forest which extend to the margin of the island.

The Control Forest Island.

The cycle shown in fig. 1 is typical for the denser type of forest island, which is not used extensively by *G. morsitans* until the hot weather compels it to evacuate the open woodland sites in favour of more sheltered conditions.

River-bed.

This breeding-ground is not used much by *G. morsitans*, as even in the hottest weather the residual forest islands can satisfy its needs.

The Experimental Forest Island.

Prior to the removal of the thicket wind-break this island was typical of the denser type, puparia only being found in the hottest weather, and its climate being almost identical with that of the Control. After the partial clearing its climate approximated to that of the Small Thickets, with the result that pupal density became maximal *before* the hot weather ; when very severe climatic conditions started, pupal density dropped and pupal mortality rose to 37 per cent. The Experimental Forest Island was no longer a perfect hot weather sanctuary such as the Control, nor was it untenable like the Small Thickets ; it was intermediate, being much hotter than the former, but a little cooler than the latter (see Table II).

Glossina tachinoides (fig. 2).

Under Logs and Palm Leaves.

Logs and Palms are used throughout the rains when all other known sites become too hot and are evacuated. In 1937 *G. tachinoides* puparia were commoner under Palms and in 1938 under Logs ; no explanation can be given. The pupal densities for these sites are very low, but they are not believed to be the major wet season breeding-grounds of *G. tachinoides*, which are still unknown (see p. 272).

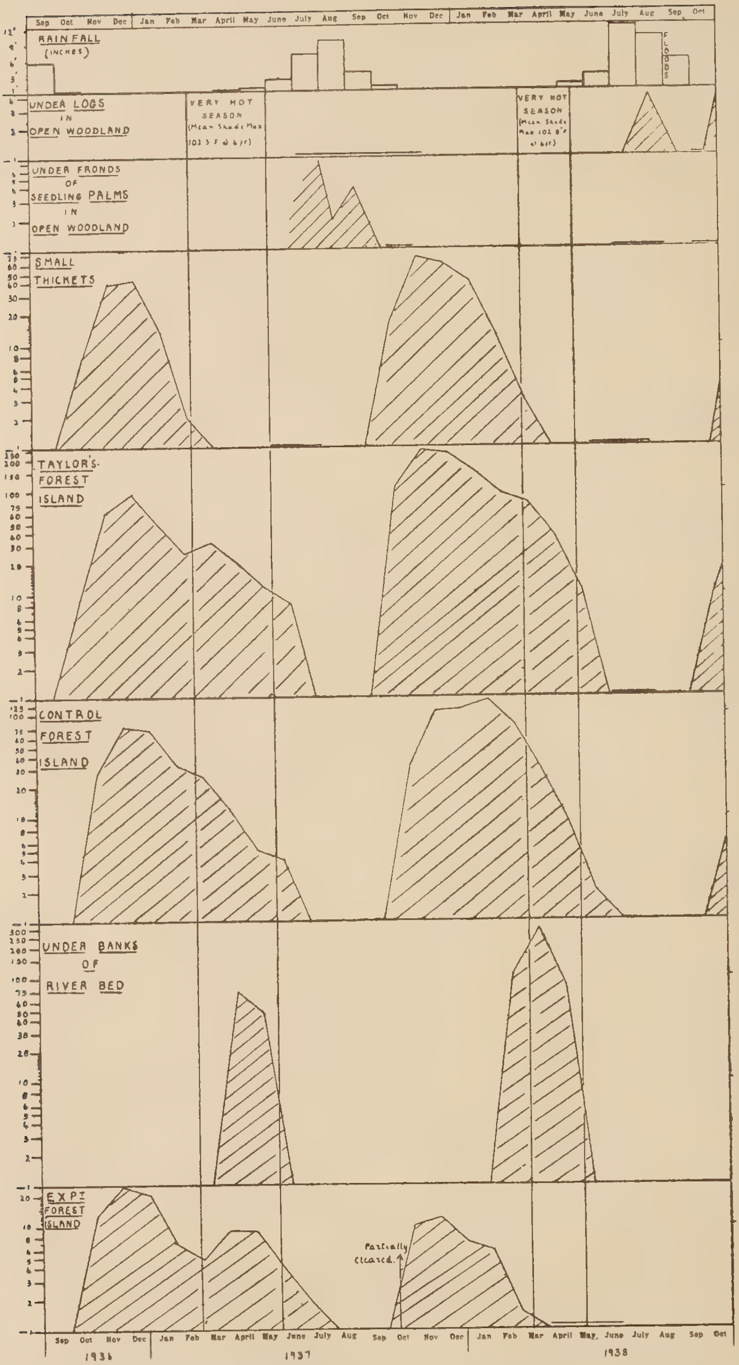

Fig. 2. The seasonal shifting of the breeding-grounds of *G. tachinoides* at Gadau, N. Nigeria.
(Pupal density expressed as puparia per boy-day of 4 hours, plotted on a logarithmic scale.)

Small Thickets.

In the early dry season (October and November) breeding shifts from the Logs and Palms into the Small Thickets, where pupal density becomes maximal in late November or December. Pupal density then starts to decrease considerably, *before* the onset of the hot weather. This decrease is not specific to the Small Thickets, but is almost universal ; although the fall starts in the cold weather of January, it continues throughout the warmer weather of February and the great heat of March and April, which suggests that temperature is not the cause. Possibly evaporation, which has been steadily rising since the end of the rains, has become unfavourably high for this species throughout the fly-belt, leading to a general reduction in adult density, or at any rate in breeding. Note how different are these results from those obtained for *G. morsitans* where breeding increased in the cooler forest islands at the expense of the warmer thickets. A local transfer took place, not a general reduction in pupal density.

To return to the Small Thickets in fig. 2 : Evacuation is complete in the hot season, when no puparia are found. Apart from a little breeding in the early rains, no more puparia can be obtained until the following dry season.

Taylor's and the Control Forest Islands.

At the end of the rains breeding starts sooner in Taylor's Forest Island, which dries up more rapidly, but otherwise both show the same cycle. Pupal density becomes greatest in the cold season and then falls steadily until the rains, when breeding shifts from the islands to the Log and Palm sites in the open woodland.

The River-bed.

As soon as the water ceases to flow, very great numbers of puparia are found under the banks of the river. It is suggested that during the preceding months even the residual forest islands were not sufficiently sheltered for *G. tachinoides*, and that when the River-bed site became available a large immigration of adults took place resulting in phenomenal pupal densities (the mean rate was 73 puparia per boy-hour in March 1938).

The microclimatic conditions under the bank of the river in the very hot months are much less severe than elsewhere. The daily evaporation in March 1938 was 22 cc. less than in Taylor's Forest Island, which was the next lowest ; the mean maximum soil temperature was 10°F. lower than in any other station ; even at 6 inches above the soil surface the mean maximum temperature was 6°F. lower than in the adjacent station in Taylor's Forest Island. The breeding-ground is destroyed when the river floods in mid-May.

Experimental Forest Island.

Prior to the partial clearing this island gave the normal pupal density cycle for a residual forest island, with the exception of a small peak in the hot weather. After the removal of the thicket wind-break the cycle continued normally until the commencement of warm weather in February, when density fell in a month to almost nothing ; the effectiveness of this island as a hot season sanctuary and breeding-ground of *G. tachinoides* had been completely destroyed.

Deductions from the Observations recorded.

It has been shown that neither species possesses a permanent breeding-ground capable of satisfying its requirements at all times of year ; instead breeding shifts from place to place. These shiftings are seasonal events which re-occur about the same time every year, forming the following cycle : In the rains breeding occurs beneath palm fronds and logs in the open woodland ; in the early dry season breeding continues in the woodland but shifts from the log and palm sites to the floor of the small thickets. At the start of the very hot weather all the woodland sites are evacuated, breeding being confined to the forest islands or river-bed. In the early rains the movement is reversed—breeding slowly shifts from the forest islands back to the small thickets, logs, and palm fronds of the open woodland. In the heavy rains puparia cannot be found in the residual forest islands, nor even in the small thickets ; breeding is confined to the logs and palm fronds.

This cycle for the shifting of the breeding-grounds fits in perfectly with the cycle for the seasonal concentration and dispersal of the adult population previously described by the writer (Nash, 1937, pp. 85–90).

It should be noted that in June all six of the available breeding-grounds are in use, indicating the widespread and extensive nature of breeding in the early rains, which leads to the maximal density and dispersal of the adults in the wet season. When the transition from wet season to dry season breeding-grounds is taking place in October, all six breeding-grounds are again in use for a short period ; undoubtedly many puparia are deposited, but their offspring are emerging into an environment that is becoming progressively more unfavourable, and adult density does not increase.

Reference to figs. 1 and 2 shows that pupal density was universally greater in the second year. This is attributed to the very low rainfall of the 1937 wet season which permitted breeding to continue without a break throughout the rains, resulting in the building up of a large stock of females for the re-population of the dry season breeding-grounds in October. Note how in every case the initial pupal densities were higher than in the previous year. Clearly, given fairly similar rates of increase in two dry seasons, the maximal density achieved will depend upon the size of the initial stock at the end of the rains. As a result of the September floods the prospects for 1938–39 are poor, the initial pupal densities for the early dry season being abnormally low.

There is a considerable difference between the reactions given by the two species to dry season climatic conditions (as was shown after the partial clearing of the Experimental Forest Island), which indicate consistently that *G. morsitans* is the hardier species. For instance, *G. morsitans* can breed in the small thickets for a month longer than *G. tachinoides*, and in the very hot weather can continue to breed freely in the residual forest islands when *tachinoides* can only do so in the river-bed. *G. morsitans* successfully avoids severe conditions by vacating one breeding-ground in favour of another ; as pupal density falls in the one, it rises in the other. *G. tachinoides* also shifts its breeding-grounds but apparently can find nowhere suitable, as pupal density decreases in *all* sites from January onwards. Admittedly when the river-bed becomes available in March *tachinoides* does find a very suitable breeding-ground which tides the species over the very hot weather, but when the river floods in May, the bulk of the new generation is destroyed.

In the wet season there must be a big difference in the breeding habits of the two species, because *tachinoides* must possess a major breeding-ground which has hitherto defied detection. Unless the species reproduces very efficiently during the rains it could not attain to its maximal adult density in August and September, nor could it produce far greater numbers of puparia than *morsitans* from the very start of the dry season. The very large initial densities recorded from the forest islands and small thickets in October and November indicate that these breeding-grounds have just been re-occupied, breeding having shifted to them at the end of the rains from some unknown site (see Oct. and Nov. 1937, fig. 2). The palm and log sites can only account for a fraction of the *tachinoides* wet season breeding, whereas they probably account for the bulk of the *morsitans* breeding.

Seasonal Pupal Mortality.

The seasonal levels of mortality, based upon the total puparia collected from all breeding-grounds, are shown in figs. 3 and 4 for both species for two years ; 1936–37 on the left, 1937–38 on the right.

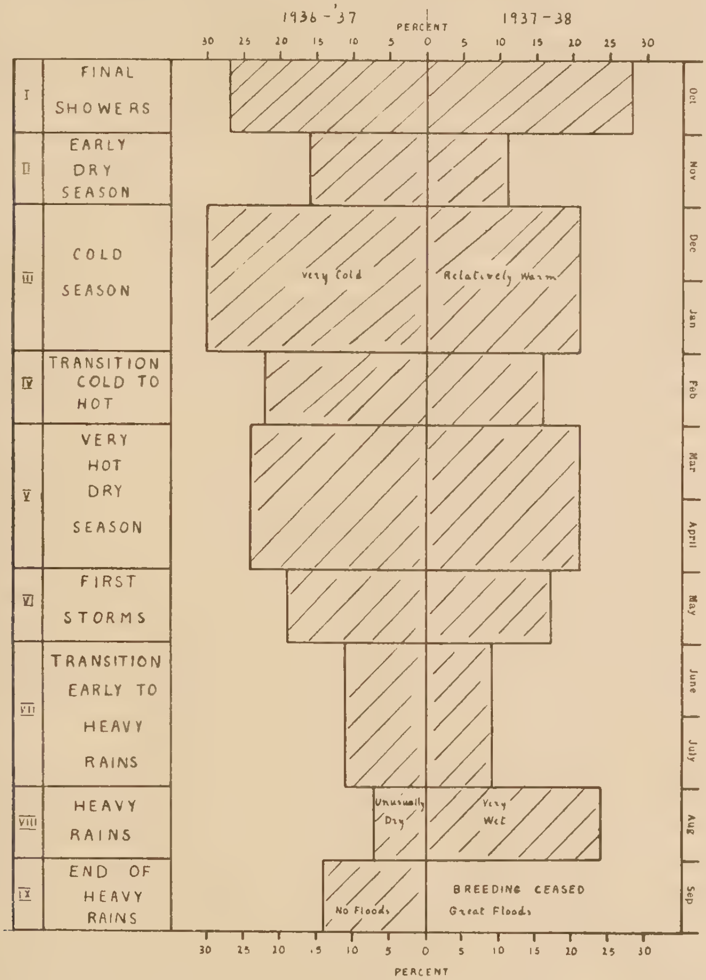

Fig. 3. Seasonal levels of pupal mortality for *G. morsitans* ; two seasons compared.
(Mortality percentages for all breeding-grounds combined.)

Glossina morsitans.

Reference to fig. 3 suggests that the seasonal pupal mortality cycle is as follows :—

I. *Final Showers* (*October*).—In the two Octobers shown the mortality is high, probably owing to the inclusion in the collection of dead puparia from September when the soil water content was unfavourably high ; but after very wet years, when there has been no breeding in September, the October puparia are all newly deposited and are very healthy.

II. *Early Dry Season* (*November*).—Pupal mortality is low.

III & IV. *Cold, and Transition Cold to Hot Seasons* (*Dec.–Feb.*).—Pupal mortality is high in the cold months, but lower in February. Note the higher mortalities of 1936–37, which was much the coldest year.

V. *Very Hot Dry Season* (*March and April*).—Pupal mortality is high at this season, and would be much higher if the adults did not evacute the warmer breeding grounds in favour of the cooler sites.

VI & VII. *First Storms to Beginning of Heavy Rains* (*May–July*).—Pupal mortality decreases steadily as the soil becomes cooler and damper.

VIII. *Heavy Rains* (*August*).—Mortality is exceedingly low in years when the rainfall is poor, but high when the rainfall is heavy.

IX. *End of Heavy Rains* (*September*).—The soil water content is greatest in this month with the result that mortality rises in dry years ; but in years of flood, breeding ceases altogether.

Broadly speaking, pupal mortality is high throughout the dry season and low throughout the wet.

The low pupal mortalities that occur during the first months of the rains must be an important factor contributing to the great wet season increase in adult density described by the writer (Nash 1937, pp. 95–99).

The higher range of mortalities occurring in the dry season must contribute to the lower adult densities observed.

The rate of mortality, in the dry season, is far lower than the writer had been led to expect from wild puparia kept in the laboratory. Very high mortality percentages only occur in the field when pupal density is very low. N.B.—The evacuation of the breeding-ground is almost complete, before the sharp rise in mortality occurs.

Glossina tachinoides.

Reference to fig. 4 shows a mortality cycle that is different from that observed for *G. morsitans*, but it is unsatisfactory owing to the small number of puparia found in the rains.

I & II. *Final Showers and Early Dry Season* (*Oct. and Nov.*).—A period of low mortality ; all puparia are newly deposited, the known sites being scarcely used by this species during the rains.

III & IV. *Cold, and Transition Cold to Hot Seasons* (*Dec. to Feb.*).—Pupal mortality is fairly high, but it would probably have been higher in the very cold season of 1936–37 if the puparia boxes had not been dug up rather too soon, allowing 7 per cent. of the emergencies to take place in the warmer laboratory. (This mistake never occurred again.)

V. *Very Hot Dry Season* (*March and April*).—Note how much lower is the pupal mortality of *tachinoides* in this severe season. The reason is that this species makes great use of the very cool and healthy river-bed site where pupal mortality is only about 6 per cent. In March and April 1938, 73 per cent. of the 3,151 *tachinoides* puparia found came from the river-bed, as against only 5 per cent. of the 1,286 *morsitans* puparia.

VI. *First Storms* (*May*).—Mortality is extremely high for *tachinoides* in May because the river comes down in flood destroying thousands of puparia. As the boxes are not dug up until news is brought that the river is approaching, it is possible to estimate the mortality by classing the puparia that had not emerged as dead ; but the figure thus obtained, and incorporated in the percentage for May in fig. 4, is considerably too low, because there are also the puparia deposited between the time of the last search and the coming down of the river. The writer estimates that about 70 per cent. of the young generation is annually destroyed.

VII. *Transition Early to Heavy Rains* (*June-July*).—Pupal mortality is low in dry years, but higher in wet. Pupal density is very low at this season; the scarcity of puparia is mainly apparent, owing to a failure to recognise the wet season breeding-grounds, but partly real, owing to the destruction in May of much of the new generation in the river-bed. Fly-round figures show that the adult density usually drops considerably in June, but it recovers, and becomes maximal in August or September.

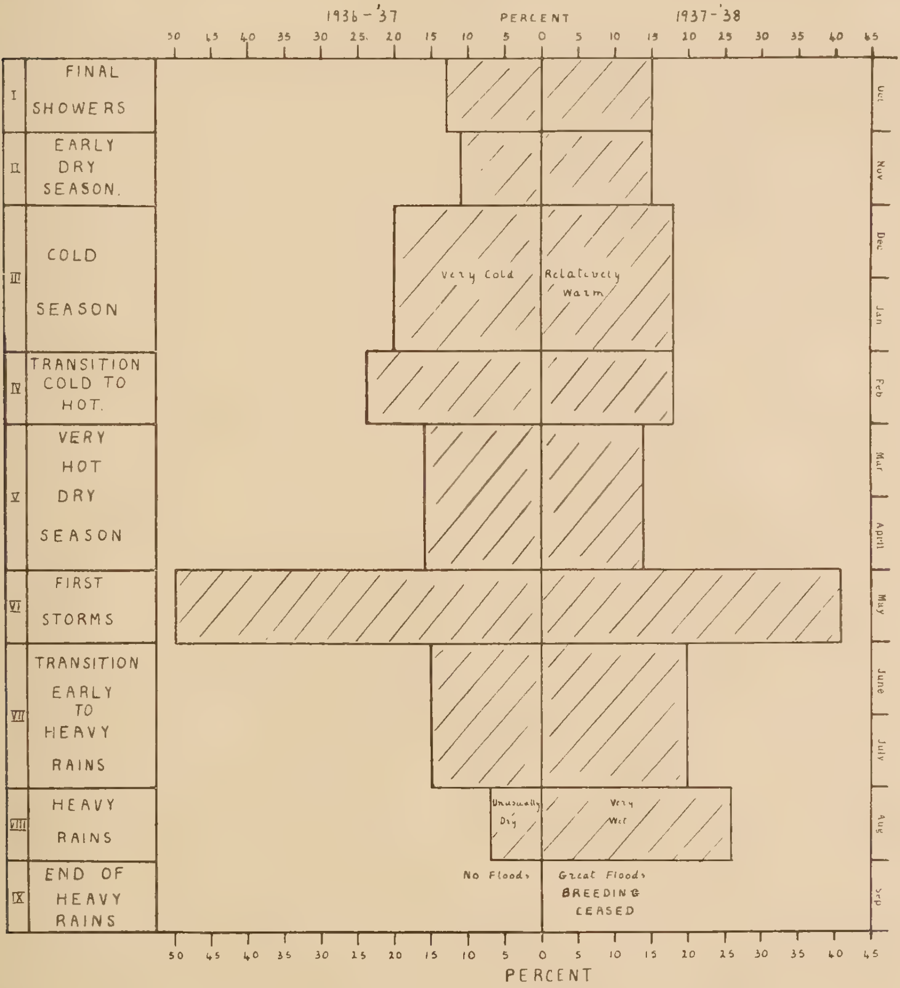

Fig. 4. Seasonal levels of pupal mortality for *G. tachinoides*; two seasons compared. (Mortality percentages for all breeding grounds combined.)

VIII. *Heavy Rains* (*Aug.*).—Pupal mortality is very low in dry years, but high in years of heavy rainfall when the soil becomes too wet.

IX. *End of Heavy Rains* (*Sept.*).—In the dry year, 1936–37, pupal mortality fell to zero, but only 34 puparia were found; in 1937–38 there were floods, and breeding ceased in all known sites for a month.

TABLE V.

Microclimatic Conditions which affect Pupal Mortality (G. morsitans).

Season	Breeding-grounds arranged in order of decreasing pupal mortality	Pupal mortality (per cent.)	No. of puparia	Soil water content at 1½in. depth (per cent.)	Mean max. soil temperature at 1½ in. depth (°F.)	Mean daily evaporation at 5 in. above surface (cc.)
I. Cold season ... A cold year (Jan. 1937)	Taylor's Forest Island	31	36	—	*74·2*	—
	Small Thickets ...	30	79	—	*73·9*	—
A warm year (Jan. 1938)	Small Thickets ...	19	95	5·4	85·6	40
	Taylor's Forest Island	17	148	3·2	78·3	35
II. Beginning of hot dry season (Feb. 1938)	Logs	—	0	3·0	*98·4*	53
	Palm Fronds	—	0	1·4	*86·5*	40
	Small Thickets ...	17	86	6·5	*89·2*	45
	Expmtl. Forest Island	17	96	5·0	*88·7*	45
	Taylor's Forest Island	15	172	3·6	*81·7*	42
	Control Forest Island	13	30	9·6	*81·3*	42
III. Very hot dry season (March–April, 1938)	Logs	—	0	2·2	*105·3*	70
	Palm Fronds	—	0	1·4	*99·4*	56
	Small Thickets ...	48	23	4·9	*95·5*	56
	Expmtl. Forest Island	36	248	4·6	*94·1*	58
	Control Forest Island	22	239	7·0	*89·0*	55
	Taylor's Forest Island	14	714	2·9	*88·7*	52
	River-bed	5*	19	5·8	*75·6*	30
IV. Transition early to heavy rains (June–July, 1938)	Control Forest Island	33	36	*26·5*	80·7	16
	Expmtl. Forest Island	20	60	*19·6*	82·5	19
	Taylor's Forest Island	16	104	*17·0*	82·3	14
	Small Thickets ...	10	39	*18·8*	82·7	18
	Palm Fronds	5	73	*11·4*	85·2	15
	Logs	4	421	*14·2*	86·4	24
V. Heavy rains (Aug. 1938)	Expmtl. Forest Island	—	—	*51·0*	77·9	4
	Control Forest Island	—	—	*50·9*	75·7	2
	Small Thickets ...	—	—	*48·2*	79·3	5
	Taylor's Forest Island	—	—	*35·5*	77·0	2
	Palm Fronds	24	42	*27·8*	79·7	2
	Logs	25	88	*32·9*	80·6	5
VI. End of heavy rains; a flood year (Sept. 1938)	Expmtl. Forest Island	—	0	*60·8*	80·8	8
	Control Forest Island	—	0	*57·9*	77·7	5
	Small Thickets ...	—	0	*52·2*	80·0	7
	Taylor's Forest Island	—	0	*41·2*	78·8	5
	Logs	—	0	*40·1*	78·8	7
	Palm Fronds	—	0	*35·7*	81·3	6
VII. Final showers (Oct. 1938)	Expmtl. Forest Island	—	0	*49·5*	83·1	20
	Small Thickets ...	—	0	*36·5*	79·7	16
	Control Forest Island	—	0	*21·4*	79·5	16
	Taylor's Forest Island	—	1	*12·4*	79·9	14
	Palm Fronds	16	25	*9·9*	83·1	13
	Logs	11	28	*16·5*	86·0	17
VIII. Early dry season (Nov. 1938)	Expmtl. Forest Island	—	0	8·2	*91·4*	31
	Palm Fronds ...	63	19	*2·0*	84·6	19
	Logs	44	71	4·9	*88·0*	25
	Small Thickets ...	24	29	10·2	83·3	25
	Taylor's Forest Island	17	6	5·2	81·7	24
	Control Forest Island	0	3	10·8	82·2	28

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* For March only.

PUPAL MORTALITY OF *GLOSSINA MORSITANS* IN RELATION TO THE MICROCLIMATE.

Microclimatic Conditions affecting Mortality of Pupae.

In Table V the breeding-grounds have been arranged in order of decreasing pupal mortality for each of the eight seasons into which the year has been divided. Against each breeding-ground is shown the mortality percentage for the season, the number of puparia upon which that figure is based, and the mean microclimatic data for the season. The climatic factor believed to be associated with pupal mortality is shown in italics. Only *G. morsitans* is dealt with, there being an insufficiency of *G. tachinoides* material throughout the wet months.

Absolute maximum temperature readings have been omitted from Table V as they only enter the critical zone for puparia (109·4° to 113·0°F.) in Seasons II and III. (Season II, Log 111·2°F. Season III, Log 113·0°F. ; Palm 111·2°F.).

The Table will now be dealt with under its seasonal divisions :—

I. *Cold Season* (*January* 1937 *and* 1938).

Data are available only for Taylor's Forest Island and Small Thickets, as elsewhere in 1937 pupal density was too low. Results for two years have been given so as to illustrate how much higher is pupal mortality in a very cold year such as 1937, when the pupal period averaged 11 days more. As mentioned on p. 266, the prolongation of the pupal period in an unsaturated atmosphere leads to increased loss in weight, which may prove injurious and account for the high pupal mortalities of the cold season.

II. *Beginning of Hot Dry Season* (*February* 1938).

There is no striking difference in the mortality percentages in the different breeding-grounds at this season ; however, mortality is lowest in the coolest site and highest in the warmest (*cf.* Mean maximum temperature). There is no breeding under log or palms. The Palm station offers a cool microclimate, but it is not made use of, as the climate of the open woodland is too severe for the adults, which are already concentrating in the forest islands.

III. *Very Hot Dry Season* (*March–April* 1938).

A good relationsip exists between the soil temperature of the breeding-grounds and the mortality of the puparia, which is least in the coolest site and greatest in the hottest. No puparia were found under palms or logs where lethal absolute temperatures were recorded. Note how pupal density is lowest in the warmest site and highest in Taylor's Forest Island which is the coolest of the usual breeding-grounds ; *G. morsitans* scarcely uses the river-bed.

Neither the soil water content nor evaporation at 5 inches show any relationship to pupal mortality or the choice of breeding-grounds at this season.

IV. *Transition Early to Heavy Rain* (*June–July* 1938).

A complete reversal has taken place. The healthiest puparia are no longer found in the coolest sites but in the driest and warmest ; breeding is shifting from the forest islands to the open woodland.

It is believed that high pupal mortality only occurs in the rains when the soil becomes too wet, and that the sites selected by the adults are always the driest available. A relationship appears to exist between mortality and temperature, but the writer does not believe that these small temperature differences, in an unimportant part of the range, are the cause of the varying mortality rates observed ; the water content is the important factor, as will be shown more clearly in the next section.

V. *Heavy Rains* (*August* 1938).

The water content of the soil has risen everywhere and now breeding persists only in the two driest sites—under logs and palm fronds. Even these two sites may be becoming too wet, as the mortality of their puparia has risen greatly.

At this season temperature would appear to be irrelevant, there being little difference between the readings from the different stations.

VI. *End of Heavy Rains* (*September* 1938).

This section marks the completion of the wet season picture in a year of very heavy rainfall when the R. Katagum finally bursts its banks and floods the river-plain. Even the log and palm frond sites have become too wet, and for a month no puparia can be found in any of the known breeding-grounds. Either breeding persists in unknown sites or a temporary cessation takes place owing to the almost saturated atmosphere ; Buxton & Lewis (1934) showed that the birth rate of *G. morsitans* is much greater at 11 per cent. relative humidity than at 44 per cent., so that one would not expect much breeding near 100 per cent. R.H.

In September 1938 the water contents of the soils in all the breeding-grounds were above their Sticky Points, and in the case of the lower-lying palm, log, and small thicket sites of the open woodland, the water content of their soils were practically up to their maximum water-holding capacities. The soils from the floors of the forest islands, which are raised up on an accumulation of humus, were further from saturation, although their water contents were much higher owing to their greater water-absorbing capacities. As will be discussed later, pupal mortality appears to be more closely related to the absolute water content, expressed as grams of water per 100 grams of oven-dry soil, than to the relative water content expressed as a percentage of the maximum water-holding capacity.

In a year of low rainfall, such as 1937, one finds that the results for September are similar to those given in the preceding section for August, breeding being confined to the log and palm sites which are the only ones whose soils give water contents of less than 35 per cent.

VII. *Final Showers* (*October* 1938).

As the river-plain dries up after the floods, breeding recommences in the driest sites. Despite the low water content of the soil in Taylor's Forest Island, *G. morsitans* prefers the logs and palms of the open woodland. Apart from preference, there would appear to be no reason why *morsitans* should not breed successfully in Taylor's Island at this season, as 86 *tachinoides* puparia were found and only 6 per cent. died. On the other hand no puparia of either species were found in the three wettest breeding-grounds. Again, neither temperature nor evaporation appears to be relevant.

VIII. *Early Dry Season* (*November* 1938).

Great caution should be observed in interpreting the data for this season as, apart from the very small numbers of puparia found, it is probable that the factor causing high pupal mortality varies according to the site. Thus very low soil water content may be the cause of high pupal mortality under palms, whereas high temperature may account for a high death-rate under logs and for the absence of breeding in the Experimental Forest Island, which had been further cleared in October. The lower mortalities occur in the cooler and damper breeding-grounds, but *morsitans* still prefers the open woodland, and scarcely uses the forest islands.

Owing to the very small number of *tachinoides* puparia found in the rains it is impossible to produce anything comparable to Table V for this species.

Temperature and Soil Water Content in Relation to Pupal Mortality.

Evidence has been given in Table V which suggests that in the dry season high pupal mortality may be caused by either too low or too high a temperature.

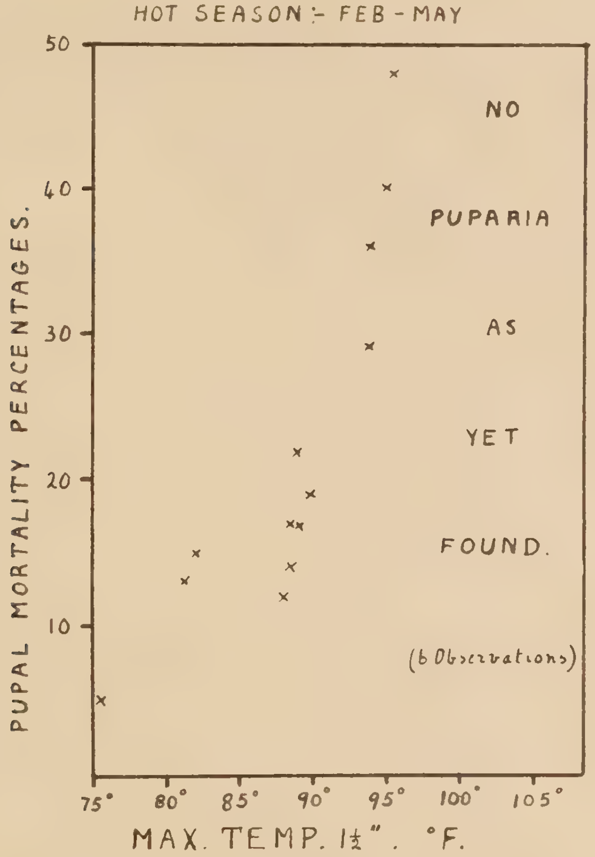

Fig. 5. Pupal mortality and mean monthly maximum temperature.

The relationship in the hot season between pupal mortality and the mean monthly maximum soil temperature is shown in fig. 5, which is based on data from Table V as well as on some from the previous year. The data are not extensive, but suggest that it is not until the mean maximum temperature rises to about 90°F. that the soil becomes too hot and mortality starts to increase. Between 90° and 96°F. mortality rises rapidly, and at temperatures above this no puparia have been found. The very low mortality at 75·5°F. relates to puparia from the damp sand of the river-bed, where the soil atmosphere is saturated ; such a low mean maximum temperature occurring in some other breeding-ground during the cold season would have been associated with a much higher mortality, but then the atmosphere of the soil would probably not have been saturated.

The relationship in the wet season between pupal mortality and the water content of the soil is shown in fig. 6. The data are not extensive but suggest that pupal mortality is low with soil water contents of 10–15 per cent., and high with water contents of 20–35 per cent., whilst in soils wetter than this puparia are not found. (Seventeen observations, representing 544 boy-hours of searching, have failed to produce puparia when the water content has been above 35 per cent.) Since, however, the soil water contents were only determined at monthly intervals, it would be wiser to avoid giving these results too precise an interpretation, and safer to conclude that puparia seem healthier in the drier soils than in the wet, and that when the soil becomes too wet puparia are not found. If the failure to find puparia in very wet soils is merely due to the impossibility of detecting them, one would have expected very high mortalities in October 1938, owing to the inclusion of puparia which had been killed in the September floods ; but the October mortalities were low, suggesting that no puparia could have been deposited in September.

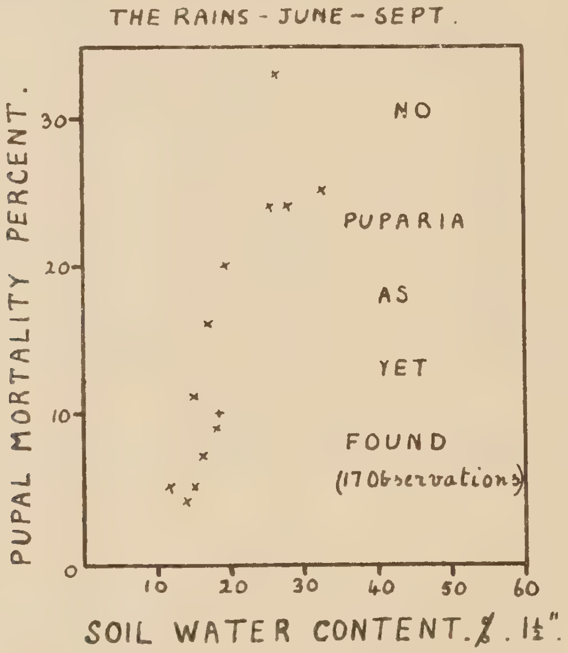

Fig. 6. Pupal mortality and soil water content.

Dr. D. Sonti suggested to the writer that, if the water content readings for each soil were expressed as percentages of its maximum water-holding capacity, one might find that mortality started to rise in all breeding-grounds when the water content reached, say, 50 per cent. of saturation ; actually no relationship could be found between pupal mortality and such relative water contents. The capacities of soils for absorbing water vary greatly ; it appears that it is the actual, rather than the relative, water content that tends to kill the puparia.

The effect exerted upon puparia by soils that are becoming unfavourably wet is unknown. The wetter the soil becomes the more air is displaced, so possibly mortality is caused by lack of oxygen ; death may occur when the water content is such that the water films between the soil particles unite to envelope the whole puparium.

The dissection of the dead puparia, which were dug up with the boxes, has shown that a higher proportion contained fully developed tsetse in the rains, than in the dry season ; the proportion is greater in very wet years such as 1938 (see Table VI).

The number of dead puparia shown for the wet season is small, partly because of low mortality and partly because breeding is scattered and fewer puparia are found. Similar figures were obtained for *G. tachinoides*.

TABLE VI.

The Stage in Pupal Life at which Death occurs in the Dry and Wet Seasons.

Year	Dry Season (October–May)		Wet Season (June–September)	
	Total dead puparia	Percentage containing fully-developed tsetse	Total dead puparia	Percentage containing fully-developed tsetse
1936–37 (poor rains)	305	24	56	41
1937–38 (very heavy rains) ...	578	26	96	63

It has been shown that the females leave a breeding-ground as soon as pupal mortality starts to increase, and that this coincides with rising soil temperature in the dry season and with rising soil water content in the rains ; but no explanation has been given as to what prompts the female to vacate a breeding-ground when she does. The writer had hoped to find a relationship with the evaporation at 5 inches above the soil surface, but as described on p. 267 evaporation is remarkably uniform in all sites at this height, and should have been measured at 4 feet. It was shown some years ago that the main dry season concentration of the adults into the forest islands, and the wet season dispersal into the open woodland, are closely related to the evaporation measured at 4 feet (Nash, 1937).

The female appears to be so well adapted to her environment that, despite rapid seasonal changes, she rarely extrudes her larva in places where the soil climate will prove fatal to her pupa. The only occasion on which the adaptation completely breaks down is when *G. tachinoides* uses the river-bed site in May, but even then the destruction of the puparia is not caused by unsuitable soil conditions, but by the mechanical effect of flood water.

THE DURATION OF THE PUPAL PERIOD.

It has been found that in the same month there may be great differences in the duration of the pupal period in different breeding-grounds, depending upon the soil temperature. Thus in the damp soil of the river-bed, which is cooled by evaporation,

TABLE VII.

To demonstrate Local Differences in the Duration of the Pupal Period of G. tachinoides.

Locality	Duration of pupal period (days)	Maximum Soil Temperature at 1½ in. Depth (°F.)		
		Mean max. temp. during pupal period	Extremes Low	High
River-bed	45	78·4	68	86
Control Forest Island	25	86·9	77	93
Small Thicket	18	94·1	92	96

one finds that the period is two and a half times as long as in the small thicket which is only about two hundred yards away. In Table VII the duration of the pupal period, together with the mean maximum soil temperature throughout that period, are given for three breeding-grounds which were searched in the first half of March 1938; the data refer to *G. tachinoides* puparia.

The duration of the pupal period may vary greatly in the same season of two different years: thus in January of the very cold season of 1937 the mean pupal period for the three forest islands was 55 days with a mean maximum soil temperature of 72·3°F.; for January 1938 the corresponding figures were 42 days and 79·5°F.

From May to July inclusive the pupal period for *G. morsitans* is very short, averaging only 22 days. This is probably an important factor in the rapid rate of increase in the tsetse population that occurs during the beginning of the rains, especially as pupal mortality has been found to be very low then (see fig. 3).

Summary.

1. The female tsetse extrudes her larva on soils ranging from fairly heavy clay to coarse sand; the presence or absence of organic matter seems to be immaterial.

2. The soil temperature varies greatly in different breeding-grounds in the dry season, but little in the rains.

3. The soil water content varies greatly in different breeding-grounds in the rains, but little in the dry season.

4. The soil water content in some of the breeding-grounds falls so low in the dry season that there can be no doubt that the atmosphere in these soils is below saturation.

5. Evaporation measured at 5 inches above ground-level varies little from site to site; bigger and important differences occur at greater heights above the ground where the screening effects of thicket become operative.

6. The seasonal changes are so great at Gadau that no one breeding-ground can satisfy the female's requirements throughout the year; instead, different breeding-places are selected for different seasons.

7. The cycle for *G. morsitans* is as follows: In the rains breeding occurs under palm fronds and logs in the open woodland. In the early dry season breeding continues in the open woodland, but shifts from the palm and log sites to the small thickets; breeding also starts in the more open parts of the forest islands. At the beginning of the very hot weather all the thickets of the open woodland are evacuated, and breeding is confined to the densest parts of the forest islands. In the early rains the movement is reversed: breeding shifts out into the open woodland, and in the heavy rains is confined to the log and palm sites.

This cycle fits in closely with the cycle for the seasonal concentration and dispersal of the adult population (Nash 1937, pp. 85–90).

8. The major wet season breeding-ground of *G. tachinoides* is unknown, but the cycle is believed to be as follows: In the early dry season breeding shifts from the log, palm, and probably from the unknown site, to the small thickets and forest islands, and becomes maximal in the cold season. Breeding now decreases in all sites, suggesting that none is really suitable—a surmise which is strengthened when tremendous breeding activity starts in the river-bed, as soon as it becomes available at the beginning of the hot season. In the early rains this site is destroyed and breeding is believed to commence in the unknown site, as it certainly does under the logs and palms.

9. It seems that in very wet years *G. morsitans*, and probably *G. tachinoides*, stop breeding for a month towards the end of the heavy rains; an almost saturated

atmosphere may be the cause. A similar phenomenon was recorded in Tanganyika (Nash 1933, pp. 190–191).

10. After a wet season of low rainfall, when there has been no cessation of breeding, the pupal density of the dry season is much greater.

11. *G. morsitans* is considered to be a hardier species than *G. tachinoides*, and to be better adapted to its environment.

12. Broadly speaking pupal mortality is high throughout the dry season and low throughout the wet, but the cycle is as follows : Immediately after the rains the soil is damp and not too hot and very few puparia die, though the percentage mortality may be increased by the inclusion of dead puparia from the end of the rains. Mortality continues low throughout the early dry season, except under logs and palms which are becoming too hot. In the cold season mortality is everywhere higher, perhaps because the prolongation of the pupal period in an unsaturated atmosphere leads to abnormal loss in weight, which may prove fatal. In the hot season pupal mortality is high for *G. morsitans* because of the high soil temperatures in its breeding-grounds, but low for *G. tachinoides* which mainly uses the river-bed site.

At the commencement of the rains the river-bed site is destroyed by flood and all the *tachinoides* puparia are killed ; elsewhere pupal mortality decreases as the soil becomes cooler and damper. Puparia continue very healthy until the soil water content becomes maximal in the last month of the rains, when mortality either rises or breeding ceases altogether, depending upon the heaviness of the rains.

13. In the hot months of the dry season breeding shifts to cooler sites when the soil temperature becomes too high ; pupal mortality is greatest in the hottest sites and least in the coolest.

14. In the wet season breeding shifts to drier sites when the soil water content becomes too high ; pupal mortality is lowest in the driest sites, and highest in the wettest.

15. Very high mortality percentages occur in the field only when pupal density is very low, because the evacuation of the breeding-ground is almost complete before the sharp rise in mortality occurs.

16. It would appear from rather scanty data that mean maximum soil temperatures between 90° and 96°F. are associated with high pupal mortality, and that at higher mean maximum temperatures no puparia are to be found.

17. Soil water contents between 10 and 15 per cent. appear to be associated with very healthy puparia, whilst with 20–35 per cent. water contents pupal mortality is very high, and at water contents above 35 per cent. no puparia can be found.

18. Pupal mortality appears to be related to the absolute, not to the relative, water content.

19. Among the dead puparia the proportion which die late in life is much greater in the rains than in the dry season ; the difference is accentuated in very wet years.

20. In dry earth pupal mortality will only be affected by the soil water content if it falls below the figure at which the soil atmosphere ceases to be saturated (Buxton, 1936) ; the figure will vary according to the nature of the soil, but even in the heavy loams of the forest islands it will have to fall below 5 per cent. before there is any possibility of the atmosphere ceasing to be saturated, and still lower in sandier soils.

21. The pupal period may vary greatly in different breeding-grounds in the same month, because water content and consequent evaporation has so pronounced an effect on the temperature of the superficial layers of the soil.

22. The short duration of the pupal period in the early rains, coupled with a very low pupal mortality and an equable climate for the emerging offspring, must

make this a particularly favourable season for the rapid increase in the size of the population.

Acknowledgments.

The writer was elected to the Avebury Studentship of the London School of Hygiene and Tropical Medicine ; this enabled him to work up his results and discuss them with Professor P. A. Buxton, to whom he is greatly indebted for both ideas and criticism given throughout the investigation, and to Mr. H. S. Leeson, Dr. C. G. Johnson and Dr. D. Sonti, also of the London School of Hygiene and Tropical Medicine, for their valuable advice.

The writer is grateful to Dr. H. M. O. Lester, O.B.E., Deputy Director, Nigerian Sleeping Sickness Service, for facilitating the investigation, and to Dr. R. Harding and Mr. D. C. Lorimer for checking the soil weighings and looking after the work in the writer's absence. Finally, mention must be made of the enthusiasm and complete reliability shown by Mallam Ibrahim who was directly in charge of the investigation, and who was ably assisted by Mallam Larwal.

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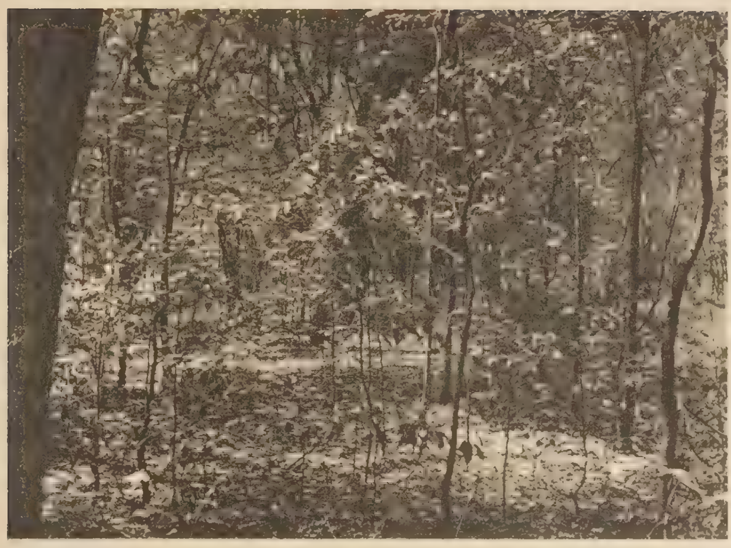

Fig. 1. *Within a residual forest island.*
N.B. *The seedling ebonies of the true forest.*

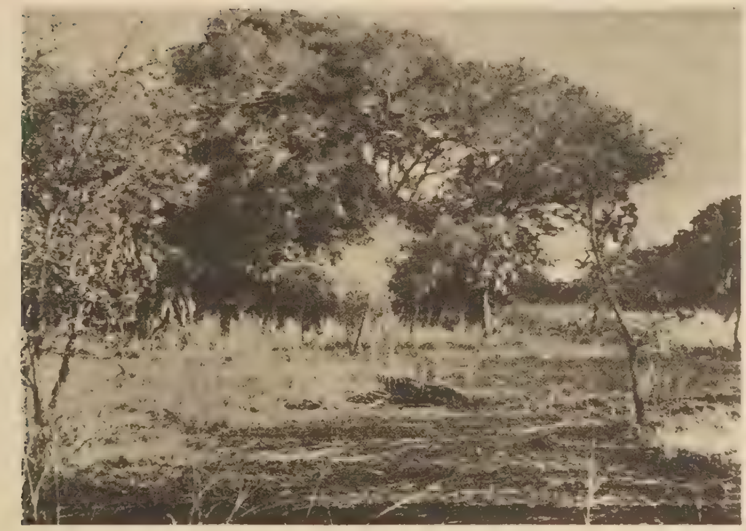

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Fig. 2. *Typical small thicket in woodland sarannah.*

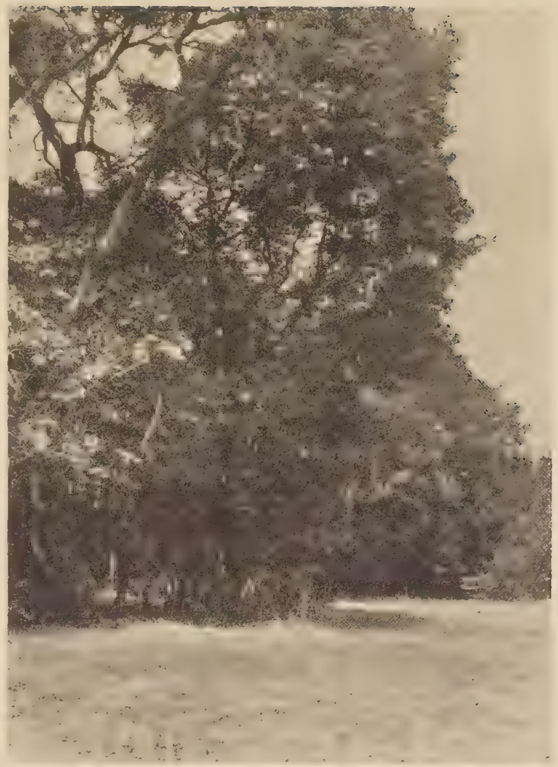

Photo by P A Buxton

Fig. 1. *In absence of peripheral thicket, a tongue of true forest extends to sharply demarcated margin of island*

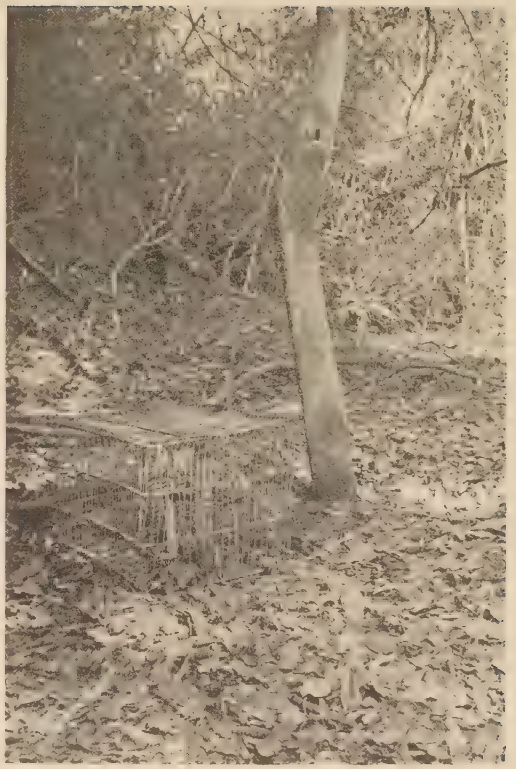

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Fig. 2. *Taylor's forest island Site of buried puparia chamber and instruments.*

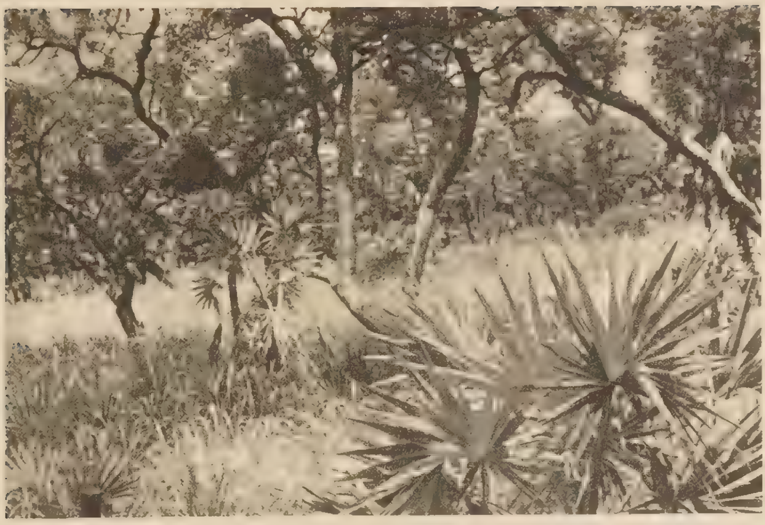

Fig. 1. *Heavy woodland savannah, in which both palm and log wet-season breeding sites occur.*

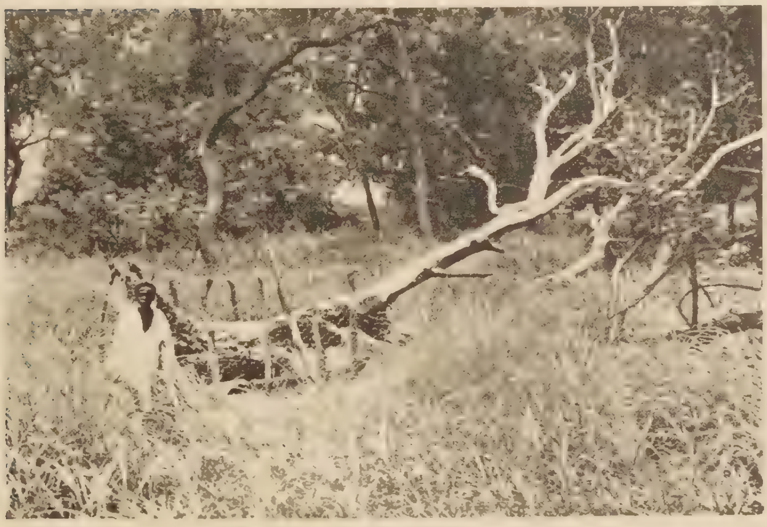

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Fig. 2. *The log station in woodland savannah.*
N.B. *Two small thickets in background.*

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st January and 31st March, 1939 :—

Agricultural Research Institute, Wad Medani :—10 Parasitic Hymenoptera, 15 Lepidopterous larvae, and 14 Mites ; from the Sudan.

Dr. W. H. Anderson :—4 Coleopterous larvae ; from the United States of America.

Mr. C. A. Bléton :—6 Diptera, 27 Parasitic Hymenoptera, and 2 Tenthredinidae ; from Morocco.

Mr. L. Boldori :—1 Coleopterous larva ; from Jugoslavia.

Mr. H. E. Box :—335 Culicidae and 500 early stages, 72 other Diptera and 200 early stages, 185 Coleoptera, 160 Hymenoptera, 11 Lepidoptera and 100 early stages, 2 species of Coccidae, 74 other Rhynchota, 2 Orthoptera, 10 Embiidae, and 3 Spiders ; from the British West Indies.

Mr. L. L. Buchanan :—14 Coleoptera ; from the United States of America.

Chief Entomologist, Pretoria :—29 Coleoptera ; from South Africa.

Father P. A. Conrads :—30 Coleoptera and 44 Orthoptera ; from Tanganyika Territory.

Mr. G. H. Corbett, Government Entomologist :—12 Diptera, 13 Coleoptera, 10 Parasitic Hymenoptera, 3 Formicidae, 8 Lepidoptera, and 18 Rhynchota ; from Malaya.

Coryndon Memorial Museum, Nairobi :—6 Tabanidae, 705 other Diptera, 725 Coleoptera, 78 Parasitic Hymenoptera, 214 other Hymenoptera, 21 Lepidoptera, 2 Rhynchota, 3 Planipennia, 16 Ticks, and 9 Crustacea ; from East Africa.

Mr. W. Cottier, Entomologist :—1 species of Coccidae and 1 species of Eriophyidae ; from New Zealand.

Mr. A. Cuthbertson, Entomologist :—74 Diptera and 4 pupa-cases, 63 Coleoptera, 7 Hymenoptera, 300 Isoptera, 25 Thysanoptera, 4 Rhynchota, 2 Orthoptera, and 150 Mites ; from Southern Rhodesia.

Dr. J. Davidson, Waite Institute :—7 Diptera, 6 Coleoptera, and 27 Parasitic Hymenoptera ; from South Australia.

Director of Agriculture, Mauritius :—5 Diptera, 15 Coleoptera, 250 Parasitic Hymenoptera, 8 other Hymenoptera, 11 Lepidoptera, and 3 species of Coccidae.

Mr. S. Duvdevani :—5 Culicidae and 7 other Diptera ; from Palestine.

Mr. Mahmoud Effat :—15 Diptera, 34 Coleoptera, 142 Parasitic Hymenoptera, and 22 other Hymenoptera ; from Egypt.

Entomologist, Mandalay :—3 Parasitic Hymenoptera and 83 Rhynchota ; from Burma.

Mr. R. G. Fennah :—2 Hippoboscidae, 30 other Diptera, 30 Parasitic Hymenoptera, 22 Rhynchota, and 10 Mallophaga ; from the British West Indies.

Dr. K. R. Fischer :—2 Diptera and 403 Parasitic Hymenoptera ; from Germany.

Mr. J. L. Froggatt, Government Entomologist :—9 Diptera, 27 Coleoptera, 154 Parasitic Hymenoptera, 15 Lepidoptera, 4 Rhynchota, and 10 Ticks ; from New Guinea.

Game Warden, Nairobi :—4 Diptera and 70 early stages, 8 Coleopterous early stages, 2 Odonata nymphs, 450 Ephemeridae and early stages, 50 Trichoptera and early stages, and 15 Perlidae ; from Kenya Colony.

Mr. J. C. M. Gardner, Systematic Entomologist :—53 Curculionidae, 14 Parasitic Hymenoptera, and 18 Lepidoptera ; from the United Provinces, India.

Mr. F. D. Golding, Government Entomologist :—4 Tabanidae and 7 Coleoptera ; from Nigeria.

Mr. J. C. Goudie :—55 Coleoptera ; from Victoria, Australia.

Government Entomologist, Coimbatore :—28 Coleoptera, 32 Rhynchota, and 4 Forficulidae ; from South India.

Government Entomologist, Kampala :—8 Diptera, 390 Coleoptera, 11 Parasitic Hymenoptera and 8 cocoons, 102 Rhynchota, 10 Orthoptera, 5 Dermaptera, 8 Planipennia, 2 Trichoptera, and 2 Perlidae ; from Uganda.

Government Entomologist, Lyallpur :—3 Diptera, 5 Coleoptera, and 18 Lepidoptera and 30 early stages ; from the Punjab, India.

Mr. W. V. Harris, Entomologist :—30 Formicidae ; from Tanganyika Territory.

Mr. G. F. Hill :—3 Isoptera ; from the Solomon Islands.

Imperial Entomologist, New Delhi :—20 Diptera and 4 pupa-cases, 98 Coleoptera, 7 Parasitic Hymenoptera, 4 other Hymenoptera, 55 Lepidoptera, 50 Thysanoptera, 38 Rhynchota, 19 Orthoptera, 2 Embiidae, and 2 Trombidiidae ; from India.

Institute for Plant Diseases, Buitenzorg :—156 Coleoptera, 7 Parasitic Hymenoptera, 55 Lepidoptera, 26 Rhynchota, and 14 Orthoptera ; from the Dutch East Indies.

Mr. E. Parry Jones, Entomologist :—66 Diptera and 66 pupa-cases ; from Southern Rhodesia.

Mr. H. Z. Klein :—4 Coleoptera and 10 Parasitic Hymenoptera ; from Palestine.

Mr. C. D. Knight :—681 Coleoptera and 228 Rhynchota ; from Kenya Colony.

Mr. R. A. Lever, Government Entomologist :—102 Diptera, 125 Coleoptera and 62 early stages, 89 Parasitic Hymenoptera, 252 other Hymenoptera, 53 Lepidoptera, 38 Isoptera, 3 Thysanoptera, 9 species of Coccidae, 1 species of Aphidae, 5 Cimicidae, 90 other Rhynchota, 2 Psocidae, 10 Orthoptera, 5 Odonata, 7 Mallophaga, 50 Mites, and 4 Millipedes ; from the Fiji Islands.

Mr. C. L. Liu :—4 Diptera, 40 Coleoptera, 43 Parasitic Hymenoptera, 5 Lepidoptera, and 3 species of Coccidae ; from China.

Dr. Ll. Lloyd :—12 Diptera ; from England and Sierra Leone.

Mr. P. Maréchal :—53 Parasitic Hymenoptera ; from Belgium.

Mr. L. Masi :—137 Parasitic Hymenoptera ; from Italy.

Mr. H. M. Morris, Government Entomologist :—3 Culicidae, 4 Nycteribiidae and 276 other Diptera ; from Cyprus.

Dr. C. F. W. Muesebeck :—1 Braconid ; from Java.

Mr. R. W. Mungomery :—1 species of Coccidae ; from Queensland.

Mr. J. Palmoni :—106 Orthoptera ; from Palestine.

Mr. F. S. Parsons, Empire Cotton Growing Corporation :—23 Parasitic Hymenoptera and 15 cocoons ; from South Africa.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—11 Diptera and 2 Ticks ; from British Somaliland.

Mr. R. T. M. Pescott :—17 Curculionidae and 1 species of Aphidae ; from Victoria, Australia.

Mr. J. S. Phillips :—1 Tachinid and 4 Coreidae ; from the Solomon Islands.

Dr. H. Priesner :—26 Parasitic Hymenoptera ; from Egypt.

Mr. S. A. Rau :—10 Diptera, 600 Isoptera, and 8 Orthoptera ; from South India.

Rhodesia Museum, Bulawayo :—71 Orthoptera from Rhodesia.

Mr. F. Schneider :—5 Lepidoptera ; from Sumatra.

Mr. F. Sein, Jr. :—60 Lepidoptera and 30 larvae ; from Porto Rico.

Mr. C. Smee, Government Entomologist :—12 Lepidoptera and 3 pupa-cases ; from Nyasaland.

Mr. F. A. Squire, Entomologist :—18 Diptera, 40 Coleoptera, 32 Hymenoptera, 6 Lepidoptera, and 27 Rhynchota ; from the British West Indies.

Dr. H. Steinitz :—100 Parasitic Hymenoptera ; from Palestine.

Stockholm Museum :—785 Coleoptera ; from Burma.

Mr. T. V. Subramaniam, Entomologist :—2 Diptera, 4 Coleoptera, and 16 Lepidoptera ; from Mysore, India.

Mr. O. H. Swezey :—1,166 Coleoptera ; from Hawaii and Guam Island.

Mr. C. B. Symes, Medical Entomologist :—1 Oestrid larva ; from Kenya Colony.

Dr. R. Takahashi :—31 Parasitic Hymenoptera ; from Japan.

Mr. Peter C. Ting :—5 Curculionidae ; from the United States of America.

Dr. A. L. Tonnoir, Senior Research Officer :—3 Coleoptera and 12 Braconidae ; from Australia.

Mr. G. C. Varley :—32 Parasitic Hymenoptera ; from England.

Mr. J. M. Waterston, Plant Pathologist :—2 Diptera, 20 Coleoptera, 5 Lepidoptera, 1,500 Isoptera, 17 Rhynchota, and 100 Psocidae ; from Bermuda.

Mr. F. G. S. Whitfield, Medical Entomologist :—2 Tabanidae, 138 other Diptera, 4 Coleoptera, 3 Parasitic Hymenoptera, 2 Formicidae, 2 Trichoptera, and 5 Ephemeridae ; from the Sudan.

Zoological Museum, Florence :—478 Curculionidae ; from various localities.

OBSERVATIONS ON COTTON STAINERS (*DYSDERCUS*) IN THE WEST INDIES.

By F. A. Squire.

Agricultural Advisory Department, Imperial College of Tropical Agriculture, Trinidad.

Introduction.

The following observations on cotton stainers were made in the Eastern Group of the West Indies, or Lesser Antilles, which extend from Trinidad to the Virgin Islands. Some idea of their size and geographical relationships will be obtained from fig. 1.

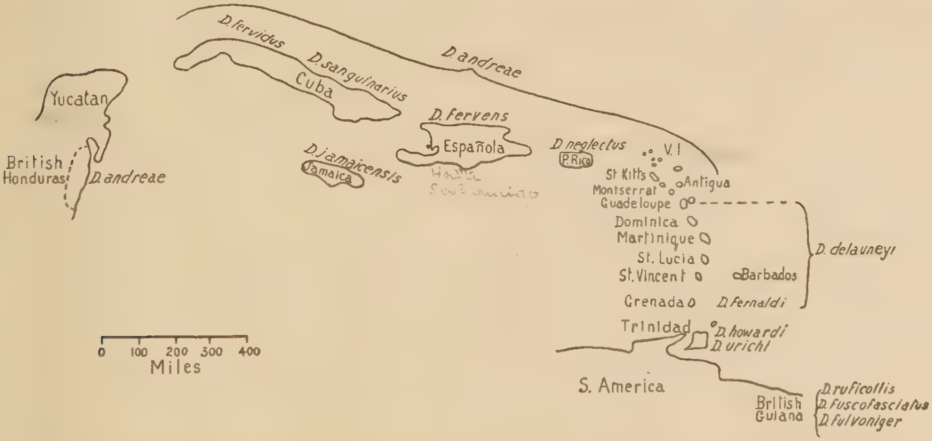
D. fervidus
D. sanguinarius
Cuba
D. andreae
Yucatan
British Honduras
D. andreae
D. fervens
Española
D. jamaicensis
Jamaica
D. neglectus
P. Rico
V. I
St Kitts
Antigua
Montserrat
Guadeloupe
Dominica
Martinique
St. Lucia
St. Vincent
Barbados
Grenada
D. fernaldi
D. delauneyi
Trinidad
D. howardi
D. urichi
S. America
British Guiana
D. ruficollis
D. fuscofasciatus
D. fulvoniger
0 100 200 300 400
Miles

Fig. 1. Showing the distribution of Cotton Stainers in the West Indies and the neighbouring British Colonies of British Guiana and British Honduras.

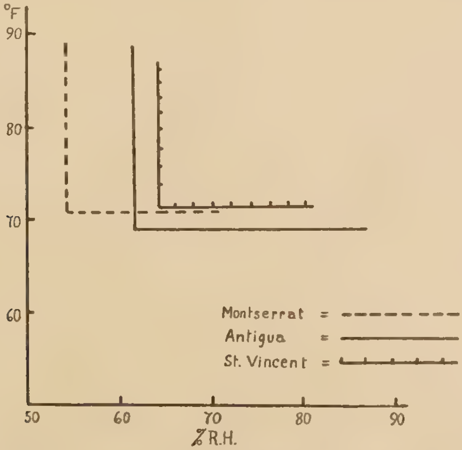

Fig. 2. Climatograph showing the range of temperature and humidity in Montserrat, Antigua and St. Vincent.

The climate is equable. The prevailing temperature and humidity for three of the islands are summarized in a climatograph (fig. 2). Two factors govern the rainfall: altitude and latitude. Most of the southern islands, being nearer the equator and having soaring mountains have a high rainfall, while some of the northern islands, being of flat or undulating aspect, are very dry. Needless to say all gradations between these extremes occur. The former have large areas of mesophytic forest; the latter are covered with dry tropical bushland of the type described by Warming[7] as "a grey, desolate, useless and scorching bushland between whose thorny, tangled shrubs and low trees one cannot penetrate without the aid of an axe," and striking xerophytic forms such as *Cereus, Melocactus, Opuntia, Agave, Acacia* and *Plumeria* are exceedingly common.

Distribution of Species.

Fig. 1 based on records by Ballou[1] and Mumford[5], and on observations by the present writer, shows the distribution of the species of *Dysdercus* in the West Indies and neighbouring countries. There is the usual multiplicity of species so common in archipelagoan faunas, the island forms totalling ten species. Of these *D. andreae*, L., is the most widely distributed, ranging from British Honduras through the Greater and Lesser Antilles as far south as Guadeloupe. It is a hardy insect and is able to withstand the extremes of heat and drought experienced in parts of the northern islands and British Honduras. *D. delauneyi*, Leth., on the other hand is a native of forest recesses and is highly sensitive to aridity. It was at one time the dominant species in Montserrat. Thus Ballou[2] writes in 1910, "It is interesting to note that in Montserrat *D. delauneyi*, Leth., has greatly increased in numbers of recent years whereas *D. andreae*, Linn., was formerly the commoner species." During the last ten years, however, *D. delauneyi* has disappeared from Montserrat, which thus seems to be on the ecological threshold for this species, whose vicissitudes may be due to the alternate destruction by hurricanes and re-growth of the mountain forests. Its absence from Barbados which lies within its range, may be explained by the scarcity of natural vegetation, the outcome of intensive cultivation.

D. fernaldi, Ballou, is confined to Grenada and *D. urichi*, Ballou, to Trinidad and both are generally rare, the common species being *D. delauneyi* and *D. howardi*, Ballou, respectively. In Trinidad there is a small dark form of *D. howardi* which Ballou[1] has described and named var. *minor*. According to Withycombe[9] this is an ecological phase occurring on secondary hosts in mountain forests, and migrants to the cotton fields laying their eggs there give rise to the larger variety. The other Trinidad species, *D. urichi*, occasionally gives rise to a form with white nymphs, which according to Harland[4] is a mutant behaving as a simple recessive to the wild type. *D. delauneyi* likewise has two extreme forms: the common one with black hemielytra, and the rare red-winged form. In addition, intermediate forms ranging from red to black are fairly common in large populations. Breeding work and field observations have shown that the red is a genetic mutant and not an ecological variety.

Host-Plants.

Plants on which stainers have been observed actively feeding and breeding in the West Indies belong without exception to the families Malvaceae, Sterculiaceae, Bombaceae and Tiliaceae.

Of the Malvaceous hosts the most important is cotton, comprising the cultivated varieties of Sea Island and Marie Galante, and two wild species, *Gossypium purpurascens* and *G. religiosum*. The former are controlled by legislation and the latter have been practically eradicated in islands where cotton is extensively cultivated. As Williams[8] has pointed out, stainers, whether on cotton or other hosts, require ripening or ripe fruits in order to multiply, so that their numbers are greatest during the ripening phase of the plant. In the case of wild cotton this occurs during the first and drier half of the year ; in the case of cultivated cottons it depends on the date of planting, which varies from island to island.

Thespesia populnea, of the same family, is a swamp halophyte and is particularly important in islands such as Antigua where the many littoral swamps, flood plains, and sluggish watercourses afford favourable conditions for its growth. It fruits perennially, and where other conditions favour breeding there is generally a permanent infestation by *Dysdercus*.

Montezuma speciosissima (*Thespesia grandiflora*) is restricted to Puerto Rico, where it is a well-known host of *Dysdercus neglectus*, Uhl., and *D. andreae*, particularly the former. It fruits towards the end or beginning of the year.

Hibiscus tiliaceus is distributed throughout the islands, occurring along the banks of streams, where it is often dominant. Adult stainers are sometimes seen huddled together on the undersides of the leaves, apparently neither feeding nor breeding.

Common Malvaceous weeds, such as *Sida cordifolia*, *S. rhombifolia*, and *Malvastrum spicatum*, are sometimes seen to be heavily infested with stainers, but generally only when cotton is present in the vicinity, and even then such infestations are as a rule very localized and short-lived. *Malachra capitata*, a common road-side and fallow weed, is a favourite host of *D. ruficollis*, L., on the coastal belt of British Guiana.

Among the Sterculiaceae the most important host is the mountain forest tree *Sterculia caribaea*. It is common on the northern part of the axial mountain range in St. Vincent where the annual rainfall exceeds 100 ins. It is also recorded from Martinique by Duss[3] but appears to be absent from the other islands. It flowers in March or April, and the first fruits dehisce and drop about September or October. By December there is generally a vast stainer population present. *S. foetida*, which occurs in the Botanic Gardens in some of the islands, has also been recorded as a host of stainers by Sands[5].

Cola sp. (probably *acuminata*), another Sterculiaceous tree, is a shade-loving mesophyte and does well in humid valleys, where it is often grown with cacao. It fruits from June to September. Stainers thrive on it, and a single tree while fruiting is able to support vast numbers.

Among the Bombaceae there are two well-known hosts of stainers. *Ochroma lagopus*, cork wood or bois flot, is commonly seen in mountain valleys in pastures and old clearings. Like *Hibiscus tiliaceus*, it is generally frequented by quiescent adults tiding over the gap between other more suitable hosts. It fruits from March to April, but stainers do not actively feed or breed on it. *Ceiba pentandra* (*Eriodendron anfractuosum*), the silk cotton tree, is common in the drier types of forest. Fruiting is erratic and does not necessarily occur every year in all individuals, but is drawn out, and for that reason where the tree is numerous it is generally able to support stainers for periods as long as six months. *Ceiba* is the most widely distributed and best known of stainer hosts in the neotropic region, and indeed one might venture to say throughout the world. Still another Bombaceous host, which has been recorded by Sands[6], is the Tobago breadnut tree, *Pachira aquatica*. This tree, also known as the wild chataigne, is common in Trinidad but rare or lacking in the other islands.

These are the main host-plants of stainers in the West Indies. Many of them are widely distributed, others are restricted to one or two islands. In general, wetter islands, such as Grenada and St. Vincent, have a greater variety of hosts than drier ones, such as Montserrat. In the latter island the eradication of one species, *Thespesia populnea*, proved a successful control measure. In St. Vincent the destruction of *Ceiba* and *Thespesia* has suppressed the insect in the greater part of the island, but in the Carib country where there still exists a complete cycle of hosts the stainer is still a formidable pest. This cycle is set forth in fig. 3.

Cola sp. is comparatively scarce and grows in accessible places. It was introduced from West Africa some 50 years ago but failed as an economic crop. To-day there are only a few scattered trees in the possession of peasants. They have been proclaimed under the existing plant protection ordinance and are being destroyed and the owners compensated. By this measure it is hoped to break the cycle of hosts and thus establish control of the stainer throughout St. Vincent.

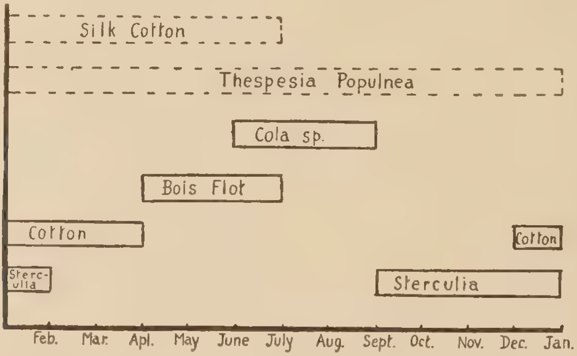

Fig. 3. Showing the fruiting periods of Stainer food plants. Those shown in entire lines represent the annual cycle in St. Vincent. Those in broken lines have been wholly or partly eradicated in most of the islands.

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A NEW *EPIPYROPS* FROM INDIA (LEP., EPIPYROPIDAE).

By T. Bainbrigge Fletcher, R.N., F.L.S., F.R.E.S., F.Z.S.

Epipyrops melanoleuca, sp. n.

♂. Expanse 8–9 (Fw. 4·5) mm. Head rather small, rounded, rather rough-scaled; whitish, irrorated with large blackish scales: viewed frontally, rather broad, eyes small but projecting slightly, space between eyes rather more than twice diameter of one eye as seen from this aspect: mouth-parts aborted, represented only by a small projecting tuft of hairs edged beneath with whitish. Antenna under half: scape short, stout, beneath with pecten of short stout bristly hairs: shaft bifid at apex, bipectinate, with 13 pairs of very long, finely-ciliated branches, each of even breadth but very slightly incrassate and spatulate at its tip; shaft white-scaled, spotted with black above point of emission of each branch; branches white, spotted with blackish and pale brown, black-brown at tips. Thorax blackish with long hair-scales. Abdomen short, not reaching tornus of hindwing, blackish, posterior margins of segments narrowly white; anal tuft small, white. Legs fuscous, tarsi lined white: foreleg without epiphysis: tibiae without spurs but with slight apical spines.

Forewing broad-triangular, costa slightly arched, more so towards rounded apex, termen oblique, gently excurved, dorsum strongly excurved on basal two-thirds; white, basal two-thirds overlaid or thickly irrorated with coarse black scales, which on the terminal third of the wing are more scattered but form (or tend to form) distinct transverse black streaks: cilia on costa short, coarse, projecting, black; from apex to tornus white, basal half compact, terminal half composed of separated coarse elongated scales; on dorsum white on exterior third of dorsum, otherwise blackish.

Hindwing about five-sixths breadth and shorter than forewing, broad-triangular, costa almost straight to four-fifths, thence downcurved to obtusely-rounded apex, termen very gently excurved to rounded tornus, dorsum gently curved; frenulum single, rather short and stout; no retinaculum; white, costal area above cell irrorated with blackish; cilia white, on costa to four-fifths black.

In one male (New Delhi) the whole of the forewing, including cilia, is blackish except for slight praeterminal patches. Two other males (Karnal, New Delhi) resemble the foregoing in the forewing, but have the hindwing, including cilia, also suffused with blackish except on dorsal area.

♀. The bipectinate antennal branches rather short, the longest about thrice width of segment of origin. Abdomen very stout, exceeding tornus, dull pink, anterior margins of segments fuscous, posterior margins with posteriorly-projecting whitish hair-scales, venter whitish. Forewing with costa strongly arched at base, fairly straight to rounded apex, termen oblique, slightly and evenly excurved to rounded (and non-evident) tornus, dorsum rather strongly excurved: white, thickly overlaid with coarse black scales, so that the whole wing appears grey-black, with a tendency to form black blotches on outer half of costal area and transverse black streaks before termen: cilia on costa composed of coarse projecting hair-scales, other cilia as in male but concolorous with forewing. Hindwing about two-thirds, elongate-ovate, costa slightly arched to (non-apparent) obtusely-rounded apex, termen oblique, evenly excurved to tornus, dorsum straight: very dark grey, cilia concolorous: frenulum simple. Two examples (New Delhi).

Another female (Karnal) has the antennal branches rather longer (4 to 5 times length of segments) but there is no other apparent difference.

Neuration.—In the forewing there is one vein missing, apparently 9 being coincident with 8; all veins well separated; 1*b* simple, 2 from rather beyond two-thirds, 3 equidistant from 2 and 4, 4 from lower angle, 5 and 6 parallel, 7 slightly diverging, 8 + 9 and 10 more approximated at base than other veins, 10 to apex, 11 from five-sixths; there is a distinct trachea along costa to a little beyond half, where this trachea bends down and is connected with 12, which reaches costa at about two-thirds; cell with two internal veins, upper from half of anterior margin to above vein 7, lower from base to below vein 6. In the hindwing all veins are well separated and about equidistant: 2 from two-thirds, 3 from before angle, 4 from lower angle, 8 free, to apex; cell with one internal vein, from base to below 6; transverse vein hardly traceable between 6 and 7 and the upper margin of cell also very weak.

In view of the known variability in neuration[3] in these species, it seems best to describe this as an *Epipyrops* in spite of the loss of one vein in forewing.

INDIA: Punjab: Karnal and New Delhi*, September–November 1937, bred by the Imperial Entomologist, India, from larvae on nymphs of *Pyrilla* sp. [presumably on sugar-cane].

Type (in B.M. Colln.) male, labelled " Imperial Entomologist 1938/40, Karnal, 1.xi.37, C.S. No. 265 "; cotypes, 5 males, 3 females.

Cocoon of pure-white silk, elongate, rather flattened, with three or four transverse dorsal ridges convex anteriorly and concave posteriorly.

It is possible that more than one species is included in the above description. Of the three females, two agree in having shorter antennal branches; the third has these longer. The males are so variable in colour-markings that no two agree exactly, but I can see no structural difference.

Dr. Hem Singh Pruthi informs me (*in litt.*) that the larvae were found " predating " on *Pyrilla* at Karnal. Exact information on the life-history would be of interest. It has been suggested[2] that the larva sucks the juices of its host. On the other hand, Professor Westwood[4] had " not the least doubt " that the larva feeds on the waxy excretion of its host; but Dodd[1], in his interesting note on the habits of Australian species, remarked that he had " never seen *frass* of the caterpillars, but in all probability the discharges are liquid and would at once roll off the waxy bodies of the hosts."

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* It is not evident whether the specimens labelled " New Delhi " were collected there or at Karnal and reared at New Delhi.

LONGEVITY OF *ANOPHELES MACULIPENNIS* RACE *ATROPARVUS*, VAN THIEL, AT CONTROLLED TEMPERATURE AND HUMIDITY AFTER ONE BLOOD MEAL.

By H. S. Leeson.

London School of Hygiene and Tropical Medicine.

The purpose of this investigation was to discover (1) how long females of *Anopheles maculipennis* race *atroparvus*, Van Thiel, would live when kept at a constant temperature and humidity after taking one initial meal of blood, and (2) whether the age of the mosquitoes at the time of taking this meal influenced their survival in such atmospheric conditions.

Observations on the longevity of mosquitoes have been published by many authors since Nuttall & Shipley (1902) stated that they had kept Anophelines alive for two to eight weeks in a moist atmosphere. Most of the accounts are concerned with mosquitoes which were allowed several or continuous opportunities of feeding during the period of observation ; some on fruit and water, others on blood (James & Shute, 1926 ; Mayne, 1930 ; Majid & Sinton, 1933 ; de Buck & Swellengrebel, 1935, and others). Some of the accounts are mainly concerned with the development or duration of infection in the mosquitoes, such as malarial infection in *Culex fatigans* or in species of *Anopheles*.

The stock culture of *atroparvus* used in the present investigations was started from larvae and adults collected in Middlesex in 1931 and is still flourishing in February 1939.

Methods.

Cages which had been prepared to receive the newly emerged adults were kept, covered with wet towels, in a constant temperature room at 25°C. (77°F.). Several trays filled with water were also kept in this room, though no precise control of humidity was attempted. Pupae, taken from stock and put into a bowl of water, were placed in the first cage and examined daily. When the first adults appeared, the bowl containing the remaining pupae was transferred to the second cage and as long as adults continued to emerge the bowl was passed on to the next cage daily, thus assuring that unfed adults of known age were obtained.

The females were given an opportunity to obtain a meal of human blood once a day. To do this the cages had to be taken from the constant temperature room to the laboratory. The period allowed for feeding was fifteen minutes, after this time those females which had fed were collected singly into numbered, open-ended tubes capped with gauze ; any remaining unfed were left in the cages which were replaced in the constant temperature room. The tubes containing the fed females were then put into vessels enclosing atmospheres of 0, 30, 60 and 90 per cent. relative humidity. These vessels were kept at the temperatures 25° and 35°C. and were examined daily, when any dead females were removed.

The experiments were done in four groups (Table I). The first was conducted between 7th February and 15th March and consisted solely of 184 fed females. In this group no record was kept of the number of adults which refused to feed. In the other groups complete records were kept of the numbers and sex of adults which successfully emerged ; of the ages and numbers of females which fed, their subsequent treatment and ages at death ; of the numbers and ages of females which died without feeding and of the dead males ; the periods were as follows : second group, 16th March to 9th April ; third group, 20th to 30th April ; fourth group, 21st June to 17th July.

TABLE I.

Numbers of adults emerged throughout each period; percentages (figures in brackets) of each sex, of females which fed and of those which died without feeding. (Totals do not include females of group 1).

Group	Date of Experiment	Adults emerged	Males	Females	Females fed	Females died (without feeding)
1	7th Feb. to 15th March	?	?	?	184	?
2	16th March to 9th April	444	207 (47)	237 (53)	141 (60)	96 (40)
3	20th April to 30th April	247	119 (48)	128 (52)	90 (70)	38 (30)
4	21st June to 17th July	623	288 (46)	335 (54)	258 (77)	77 (23)
	Totals	1,314	614 (47)	700 (53)	489 (70)	211 (30)

Results.

It will be observed (Table I) that in each group males are slightly fewer than females and that the difference is very regular (46–48 per cent. males in all groups). As the female larval stage lasts longer, females are more at risk than males and the discrepancy is probably greater still in early stages. Tested statistically however (by χ^2) the differences appear to be not greater than might be expected to occur by chance.

TABLE II.

Numbers of unfed males which died at each age, and the percentages which died on the second day after emergence and which died in the first three days after emergence.

Group	Age at death in days										Total Males
	0	1	2	3	4	5	6	7	8	9	
2	4	38	106 (51%)	46	10	2	0	0	1	0	207
			93%								
3	3	3	49 (41%)	41	16	7	0	0	0	0	119
			80%								
4	0	10	77 (27%)	74	51	46	18	3	5	4	288
			56%								
Totals	7	51	232 (38%)	161	77	55	18	3	6	4	614
			73%								

Inspection of the figures for the females which fed shows that an increasing percentage of females took a blood meal. The differences between the numbers of those which fed and those which died without feeding are statistically significant.

The figures for males in Table II show that a large proportion of males died in the first three days after emergence, and that the percentage of males found dead during these three days became smaller in each succeeding group (93, 80 and 56 per cent.). The greatest daily mortality in each group occurred on the second day and this figure also became less in the third and fourth groups (51, 41 and 27 per cent.).

TABLE III.

Numbers of unfed females which died at each age, and the percentages which died on the second day after emergence and which died in the first three days after emergence.

Group	Age at death in days										Total Females
	0	1	2	3	4	5	6	7	8	9	
2	2	22	52 (54%)	15	4	1	0	0	0	0	96
			95%								
3	1	7	16 (42%)	9	2	2	1	0	0	0	38
			87%								
4	0	5	19 (25%)	13	16	11	4	0	5	4	77
			48%								
Totals	3	34	87 (41%)	37	22	14	5	0	5	4	211
			76%								

The figures for the unfed females (Table III) resemble those for the males. The considerable seasonal difference in the material cannot yet be explained or controlled, but as the difference has at any rate been established, the fed females will next be examined.

Of the total number of females which fed (Table IV) more than 82 per cent. had taken a blood meal by the third day after emergence; the highest daily figure, 35 per cent., occurred on the second day.

It will be remembered that the first group consisted solely of fed females; it is therefore not strictly comparable with the other groups. In this group, 78 per cent. fed in the first three days, the largest daily percentage, 36 per cent. on the second day. In the other groups, the greatest daily percentages were: second group, 60 per cent. on the *first* day; third group, 40 per cent. on the second day; and fourth group, 37 per cent. on the second day after emergence.

TABLE IV.

Numbers of females which fed at various ages, and the percentages which fed on the second day after emergence and which fed during the first three days after emergence.

Group	Age when fed, in days										Total Females
	0	1	2	3	4	5	6	7	8	9	
1	0	18	67 (36%)	59	21	19	0	0	0	0	184
			78%								
2	0	84 (60%)	46 (33%)	11 (7%)	0	0	0	0	0	0	141
			100%								
3	0	22	36 (40%)	24	5	3	0	0	0	0	90
			91%								
4	0	14	96 (37%)	79	43	17	6	2	0	1	258
			73%								
Totals	0	138	245 (35%)	173	69	39	6	2	0	1	673
			82%								

TABLE V.

Numbers of females which fed at various ages and the mean survivals in days (figures in brackets) when kept at 25°C. (77°F.) and various relative humidities.

Percent. R.H.	Age when fed (in days)										Totals	Survival	
	1		2		3		4		5				
	No.	Days survived	No.	Days survived	No.	Days survived	No.	Days survived	No.	Days survived		Mean	Max.
0 ...	13	(3·4)	29	(3·1)	40	(3·6)	11	(3·6)	7	(3·1)	100	(3·4)	6
30 ...	28	(4·7)	46	(5·3)	18	(4·8)	4	(3·5)	4	(3·5)	100	(4·9)	8
60 ...	41	(5·7)	33	(5·9)	22	(5·9)	6	(5·2)	6	(4·7)	108	(5·7)	11
90 ...	42	(7·4)	41	(9·3)	14	(8·1)	5	(7·5)	5	(9·7)	107	(8·3)	14
Nos. fed at at each age	124		149		94		26		22		415		
Percentage fed at each age	30		36		23		6		5		100		

Mean Survivals of Fed Females at 25°C.

It is plainly shown in Table V that humidity influences survival ; females kept at the higher humidities lived longer than those kept at the lower humidities ; but in considering whether the age at which the mosquitoes fed influenced the survival times, two points will be noticed. Firstly, it is clear that life at 0 per cent. relative humidity was so short that the age when the females fed made no difference to their survival, and secondly, that so few females lived for 4 and 5 days before feeding that the numbers available in these age groups are insufficient to enable reliable conclusions to be drawn.

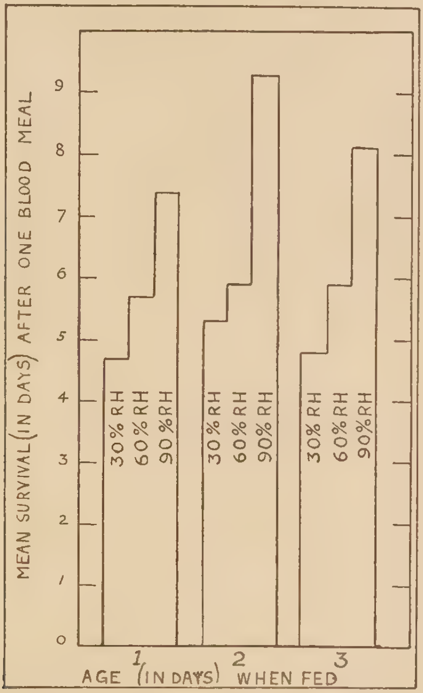

Fig. 1. *A. maculipennis* race *atroparvus*; mean survivals (in days) at 25°C. (77°F.) and various humidities after one blood meal.

There remain those females which fed on the first three days of adult existence and those of them which were distributed among the relative humidities of 30, 60 and 90 per cent. (fig. 1). The differences between adjacent pairs of mean survival times at the same relative humidities were tested by χ^2. It was found that the differences between the survival times of fed females kept at 30 per cent. relative humidity was statistically significant by conventional standards, which suggests that the longer mean survival of those females which fed on the second day, as compared with those which fed on the first and third, was real and that the differences were not likely to be due to chance. The differences between mean survivals at 60 per cent. relative humidity were very small, and not significantly different. At 90 per cent. relative humidity there is a significant difference between those fed on day 1 and day 2; but that between those fed on days 2 and 3 is not significant.

The evidence regarding the second day after emergence shows that this day is a critical one in the life of *Anopheles maculipennis* race *atroparvus*. Under identical conditions, more adults of both sexes died on this day than on any other, more females fed on this day than on any other, and those which fed on this day lived longer than those which fed on any other day.

The remainder of the fed females (258) were kept at 35°C. and behaved similarly, though the survivals were of course considerably shorter.

I am permitted to record that *Culex fatigans* with which Professor Buxton experimented in the same way gave similar results ; the chart (fig. 2) illustrates how fed females kept at higher humidities lived longer than those kept at lower humidities.

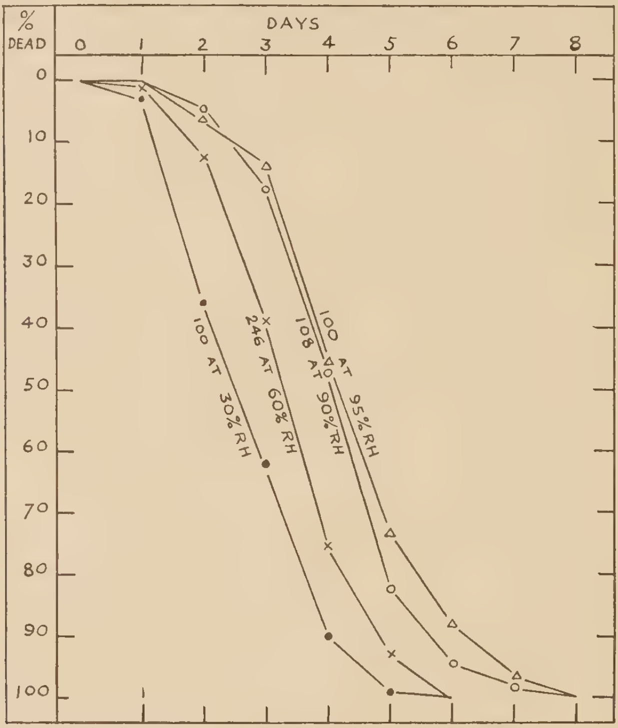

Fig. 2. *Culex fatigans* ; Percentages of females dead each day when kept at 23°C. (73·4°F.) and various humidities after one blood meal.

Summary.

From January to July 1938, experiments with *Anopheles maculipennis* race *atroparvus*, Van Thiel, were undertaken to discover whether humidity and the age at which the females fed influenced their longevity. It was found that they lived longer at higher than at lower humidities ; that most of the females which fed did so in the first three days ; that those which fed on the second day after emergence lived longer than those which fed at other ages ; and that the feeding period was slightly extended in the later experiments, though only a small proportion lived long enough to take their first blood meals on the fourth and fifth days.

Rather more than 50 per cent. of each batch of newly emerged adults were females.

A large proportion of the deaths of unfed males and females occurred during the first three days, most of them on the second day ; this mortality decreased in successive experiments. which were carried out [illegible] later in the year ?

Culex fatigans, Wied., behaved similarly.

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CORFU *PHLEBOTOMUS* (DIPT. PSYCHOD.) FOUND IN HUMAN HABITATIONS.

By Theodore Stephanides.

The first *Phlebotomus* of the year 1936 observed in Corfu, Ionian Islands, Greece, was seen on 15th June. From that date these Diptera became rapidly more numerous (maximum towards the end of June and beginning of July) and disappeared fairly suddenly in the second half of September, not one being seen after the 21st of that month.

In the town of Corfu itself, the *Phlebotomus* were collected in the author's flat (3rd floor of a house surrounded by a garden) three times a day: 7–8 a.m., 1–2 p.m. and 11–12 p.m., so far as possible.

Almost all were captured in the three bedrooms and only a few in the passages and the w.c. None was obtained from the study, the dining-room or the drawing-room, although these often remained with the windows open and the lights on until after midnight.

The first series of observations was made between the 15th June and the 3rd July, 228 *Phlebotomus* being captured: 216 *P. papatasii* (153 males, 63 females), 5 *P. perniciosus* var. *tobii* (2 males, 3 females), 4 *P. minutus* s. str. (1 male, 3 females) and 3 *P. parroti* (3 males).

The *P. papatasii* were encountered by day and by night in more or less equal numbers; the other species only during the day.

Between the 2nd and the 29th August, the observations were continued in a country-house at Kalami, a village situated on the N.E. coast of the island, about 15 kil. N. of the town. The Diptera were collected at the same hours as before.

This time 189 *Phlebotomus* were caught: 118 *P. papatasii* (65 males, 53 females), 69 *P. major* (26 males, 43 females), 1 *P. perniciosus* var. *tobii* (1 female) and 1 *P. sergenti* (1 female). Once again the *P. papatasii* were met with in approximately equal numbers by day and by night. With six exceptions, the *P. major* were taken by night. The *P. perniciosus* var. *tobii* was captured in the morning and the *P. sergenti* at night. The *P. papatasii* were mostly collected in the bedrooms, the *P. major* in the dining-room and kitchen in the circle of light cast by the oil-lamps.

Between 30th August and 21st September the observations were resumed in town and yielded 60 *Phlebotomus*: 54 *P. papatasii* (37 males, 17 females), 3 *P. parroti* (3 males), 1 *P. perniciosus* var. *tobii* (1 female), 1 *P. minutus* s. str. (1 female) and 1 *P. major* (1 female). The *P. papatasii* were met with as before, the other species during the day.

Finally Dr. D. Goussis was kind enough to send the author, from the extreme S. of the Island, 11 *Phlebotomus* taken between 1st and 15th September. These were all *P. papatasii* (5 males, 6 females).

In the year 1937 the first *Phlebotomus* was caught on 18th May at Palaeocastritsa, a locality situated on the N.W. coast of Corfu, and the last at the same place on 3rd October. In addition to this locality collections were also made in the town of Corfu and near the village of Kontokali, about 6 kil. N.W. of the town, the total number of specimens secured being 578.

Out of a total of 1,066 *Phlebotomus* (488 for 1936 and 578 for 1937) obtained from six different localities in the Island, the following numbers were found for each species:—

1.	*P. papatasii*, Scopoli 1786	526	males	271	females	=797
2.	*P. major*, Annadale 1910	72	,,	100	,,	=172
3.	*P. sergenti*, Parrot 1917	27	,,	31	,,	= 58
4.	*P. minutus*, Rondani 1843, s. str.	11	,,	15	,,	= 26
5.	*P. perniciosus*, Newstead, var. *tobii*, Adler, Theodor & Lourie 1930	3	,,	4	,,	= 7
6.	*P. parroti*, Adler & Theodor 1926	6	,,	0	,,	= 6

From these figures it is clear that *P. papatasii* is by far the most abundant species in Corfu, so far as human habitations are concerned. *P. major* and *P. sergenti* are fairly plentiful in the country, but extremely rare in town. *P. minutus* s. str., *P. perniciosus* var. *tobii*, and *P. parroti*, are very rare in all localities. These 6 species are the only ones which have been observed in the Island by the present author. *P. papatasii* is met with in about equal numbers throughout the 24 hours. *P. minutus* s. str., *P. perniciosus* var. *tobii*, and *P. parroti* are found during the day. The remaining two species are most frequently captured at night.

It is strange that *P. chinensis*, Newstead 1916, plentiful in other parts of Greece and recorded by various authors as one of the commonest species in Yugoslavia, seems to be non-existent—or at any rate very rare—in Corfu.

A NEW SPECIES OF *DIEUCHES*, DOHRN (HEM. LYGAEIDAE) INJURIOUS TO STRAWBERRIES IN TASMANIA.

By J. W. Evans, D.Sc.

I. K.

The Lygaeid bug described below has been well known as a pest of strawberries in Tasmania for a long time, both Thompson (1895) and Lea (1908) having given particulars of its activities under the name of the " Strawberry Bug." Lea mentions that it also occurs in Victoria and New South Wales, but as it belongs to a cosmopolitan genus with a world-wide distribution, it is possible that the Tasmanian species is distinct.

These insects may be found in abundance under plants growing in rockeries, and in other situations where there is an accumulation of dead dried vegetation. Strawberry plants thus provide a favourable habitat. The bugs feed on ripe and ripening fruit and cause distortion and discoloration of the berries as well as imparting a disagreeable taint.

Dieuches raphaeli, sp. n. (fig. 1).

Length, 6 mm. (from the tip of the head to the apex of the abdomen). General coloration, black with brown and yellowish-white markings.

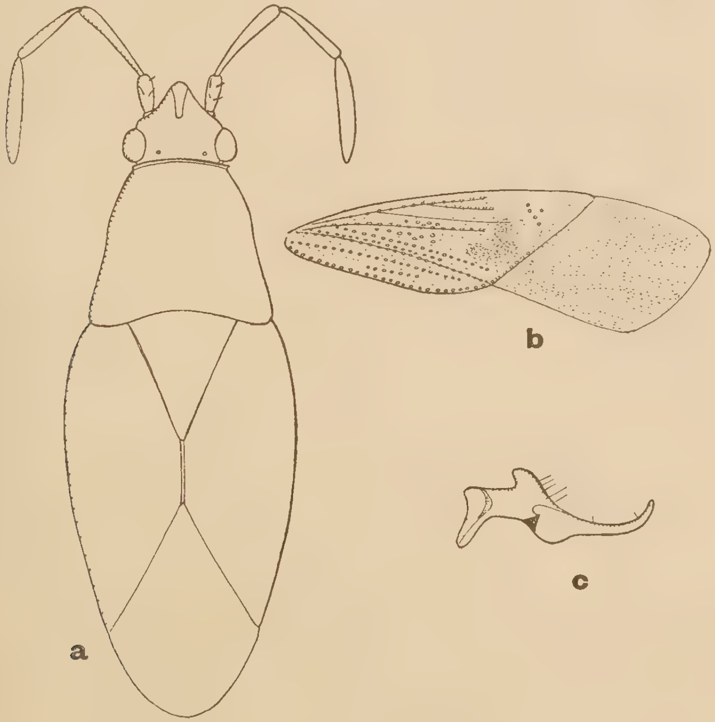

Fig. 1. *Dieuches raphaeli,* sp. n.: **a**, adult; **b**, hemielytron; **c**, male genital clasper.

Head, black, pilose, but for the antennae and the labium. Antenna, basal segment black with a few small strong spines ; second segment, proximal two-thirds pale brown, distal third dark brown ; third segment, proximal third pale brown, distal two-thirds black ; apical segment basally black, followed by a pale yellowish-white band, remainder black. Labium reaching as far as the coxae of the middle pair of legs, proximal segment black, brown apically ; second segment brown ; two distal segments black. *Pronotum*, punctate, anterior two-thirds black, but for the collar-like anterior margin, which is dark brown ; posterior two-thirds marked with an irregular pale yellowish-brown and chestnut or dark brown pattern. *Scutellum*, black. *Hemielytra* (fig. 1, *b*), corium and clavus concolorous with the posterior third of the pronotum, punctate, the pits principally following the courses of the veins ; membrane dark brown or black, veins whitish-hyaline. *Thorax*, ventral surface black, but for the episterna and epimera of each segment, which are yellowish brown, and the legs of which the proximal third or two-thirds are brown. *Abdomen*. Ventral surface, black. Male genital clasper as in fig. 1, *c*.

Type ♂ from Margate, Tasmania (*T. Raphael*), in the collection of the Australian Museum, Sydney. Paratype in the British Museum.

A brachypterous form also occurs, but is infrequent.

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THE *EPHIALTES* (HYM. ICHN.) PARASITISING THE CODLING MOTH.

By J. F. Perkins, B.Sc.

Department of Entomology, British Museum (Natural History).

The *Ephialtes* which have been bred from the codling moth, *Cydia pomonella*, L., have usually been determined as *Ephialtes* (*Calliephialtes*) *extensor*, Taschenberg 1863. Two species have been confused under this name, and neither of them is *E. extensor*, which, from the description and from material examined in the Brauns and Thomson collections, is a synonym of *Ephialtes punctulata*, Ratzeburg (=*Pimpla punctulata*, Ratz. 1844) (syn. nov.). The type of the latter species has been examined, as have the types of *Ephialtes caudata*, Ratzeburg 1848, and *E. crassiseta*, Thomson 1877, which are the two species that were actually bred from the codling moth. These species may be readily distinguished by the relative lengths of the segments of the hind tarsi and also in the female by the form of the ovipositor. The following key distinguishes the three species mentioned above.

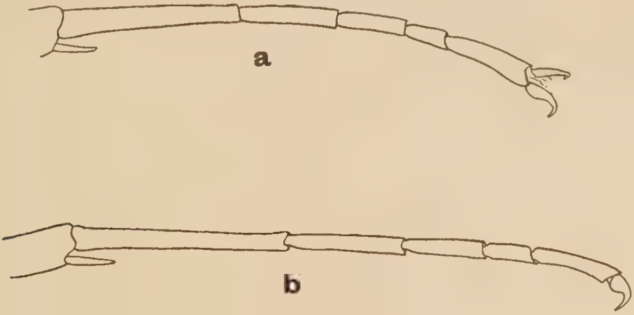

Fig. 1. Hind tarsus of male of : **a**, *E. caudata*, Ratz. ; **b**, *E. punctulata*, Ratz.

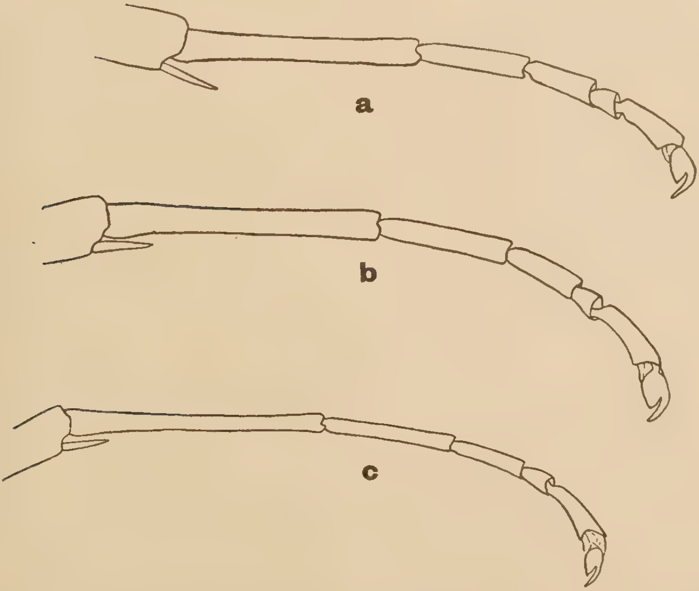

Fig. 2. Hind tarsus of female of : **a**, *E. crassiseta*, Thoms. ; **b**, *E. caudata*, Ratz. ; **c**, *E. punctulata*, Ratz.

Females.

1. Ovipositor obliquely truncate apically (fig. 4*a*) ; (hind tarsi viewed dorsally, with the 4th segment as long as apically broad)....................*caudata*, Ratz.
—. Ovipositor sharply pointed apically (fig. 4*b*)..2
2. With a long, distinct, yellow line in the hind angle of the pronotum ; hind tarsi viewed dorsally with the 4th segment about $1\frac{1}{4}$ times as long as apically broad, the legs long and slender (fig. 2*c*, 3*c*).............................. *punctulata*, Ratz.
—. At most with a very short yellowish line in the hind angle of the pronotum ; hind tarsi with the 4th segment as long as apically broad, legs distinctly thicker (fig. 2*a*, 3*a*)..*crassiseta*, Thoms.

Males.

1. Pronotum with a yellow line in the extreme hind angle ; the genital claspers not strongly produced apically......................................*crassiseta*, Thoms.
—. Pronotum with a long yellow line in the hind angle, reaching nearly as far as the notauli ; genital claspers strongly produced..2
2. Hind tarsi less elongate (fig. 1*a*) ; the 4th segment, viewed dorsally, about twice as long as apically broad and a little less than half as long as the apical segment... *caudata*, Ratz.
—. Hind tarsi more elongate (fig. 1*b*) ; the 4th segment nearly three times as long as apically broad and more than half as long as the apical segment .... *punctulata*, Ratz.

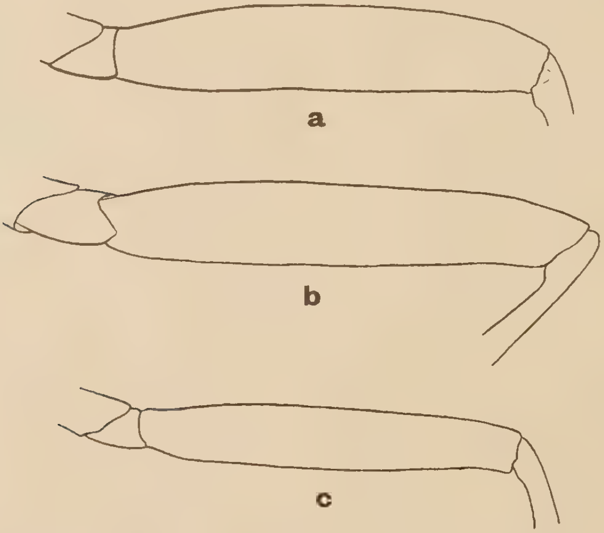

Fig. 3. Hind femur of female of : **a,** *E. crassiseta,* Thoms. ; **b,** *E. caudata,* Ratz. ; **c,** *E. punctulata,* Ratz.

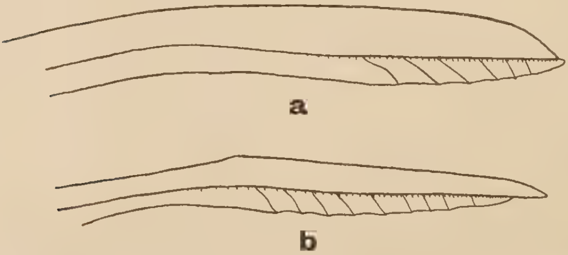

Fig. 4. Apex of ovipositor (lateral) of : **a,** *E. caudata,* Ratz. ; **b,** *E. punctulata,* Ratz.

CONTRIBUTION TO THE PHYSICAL ECOLOGY OF *TORTRIX POSTVITTANA*, WALK. (LEP.).

By L. J. Dumbleton.

Division of Entomology, Department of Scientific and Industrial Research, Cawthron Institute, Nelson, New Zealand.

1. The Velocity of Development in relation to Temperature.

(*a*) *Methods.*

The experiments at temperatures above room temperature were carried out in thermostatically controlled incubators which had a range of ±1°C. about the mean temperature. The experiments at temperatures below room temperature were carried out in a multiple temperature incubator. The insulation of this apparatus was not efficient enough to give a constant temperature unless the room temperature was constant. The room temperature fluctuated considerably, and the extreme fluctuations of the temperature about the mean were of the order of ±3°C. The mean temperature given is the mean of the daily recordings of the incubator temperatures.

An attempt was made to standardize the humidity conditions at different temperatures. For this purpose "saturation deficiency" (S.D.) was maintained constant in preference to relative humidity, as the former gives comparable indices of the evaporative power of the air at different temperatures. All experiments were made under conditions designed to give a S.D. of 3 mm. of Hg. In Table I are shown the solutions used to give the required S.D. at the different temperatures.

TABLE I.

Solutions used to give a S.D. of 3 mm. of Hg.

Approximate temperature °C.	Solution	Relative humidity per cent.
12	NH_4NO_3 saturated	73
16	NaCl ,,	77·5
20	$(NH_4)_2SO_4$,,	81·7
25	KOH (S.G. 1·130)	87·5
30	KOH (S.G. 1·110)	90
35	KOH (S.G. 1·095)	92·5

In the case of the experiments carried out in the multiple temperature incubator the humidity was controlled by suspending the experimental material over a saturated solution of the appropriate salt in a tightly closed glass jar 3 ins. in diameter and 2½ ins. in height. Inside the jar the material was isolated in short lengths of glass tubing 1¼ in. in length by ¼ in. in diameter and closed at both ends with cottonwool plugs. In the case of the experiments carried out in the larger incubators, the material was isolated in glass tubes or vials stopped with cottonwool plugs and placed in a desiccator containing solutions of KOH designed to give the required S.D. The daily introduction of fresh food in the experiments with larvae disturbed the moisture equilibrium at least temporarily, but it was felt to be desirable to control the humidity factor as far as was possible under the conditions.

The larvae were fed daily. A strip of apple leaf was inserted into the tube and the residue of the previous day's food was removed. Preliminary experiments showed that food quality was a factor governing the rate of development of the larvae. For this reason the experimental larvae were fed on mature apple leaves, as young leaves would probably not be available during the late summer. The mortality amongst the larvae was apparently of no importance until the upper limit of the medial temperature range (about 30°C.) was reached. At lower temperatures the mortality was largely due to accidents incidental to handling. It is possible that the daily changing of the food, especially when the larvae were small, may have retarded their growth owing to the daily destruction of the webs which they constructed.

The space available in the multiple temperature incubator allowed of only two jars being used in each compartment. As each jar would hold only 10 tubes, the number of larvae at each temperature was limited to 20, though larger numbers of egg-masses and pupae could be reared in each jar. The two lots of larvae at 19·6° were treated as duplicates.

The egg-masses were obtained by caging male and female moths, collected from the field at Adelaide, in glass tubes 3 in. in length and $\frac{7}{8}$ in. in diameter. These were lined with cellophane on which the eggs were laid. The tube was stopped with a cottonwool plug, in which was inserted a short glass vial containing honey solution. The eggs were laid at temperatures between 20° and 25°C. The larvae, with the exception of those at 25° and 35°C., were derived from eggs sent from Tasmania by Mr. J. W. Evans. Those used at 25° and 35° were the progeny of adults taken in the field at Adelaide. The pupae used at temperatures of 19·2°C. and over were derived from larvae which had been reared at the same temperatures. Those at 15·8°C. were mostly reared at the same temperatures but included 6 which were placed at 15·8 a few days before pupation. Those at 12°C. were all derived from larvae which had been reared at 25° and placed at 12° a few days before pupation. The pupae at 6° were derived from last instar larvae which had been starved at low temperatures. These latter pupae were at a S.D. of 0–1 mm. and not at 3 mm. as was the remainder of the material.

The time of deposition of the eggs was known within 12 hours and the incubation period was calculated from the beginning of this period. The time of hatching of the first larvae from each egg-mass was known within 24 hours and the incubation period was calculated to the end of this period. The incubation period recorded is the mean of the times of first hatching of each of the egg-masses in the experiment. The length of the larval period was taken as the period between the commencement of incubation and the time when pupation was observed to have occurred. The larvae at 25°, 30° and 35° were caged and incubated within 24 hours after hatching and were inspected for pupation at 24 hour intervals. The larvae at 11·7°, 15·7° and 19·6° were possibly 2 days old (but unfed) before incubation commenced. The time of pupation and emergence of adults was known to within 24 hours in the experiments below 20°C. In the experiments at 25° and 30°C., the time of pupation and emergence was known to within 12 hours.

(*b*) *Results.*

TABLE II.

Incubation Period of Eggs.

Mean temperature °C.	Extreme range of temperature	Number of egg-masses	Mean incubation period in days	Standard error in days	Percentage development per day
11·0 ...	8·0–13·8	11	25·2	0·248	3·97
16·0 ...	14·0–18·0	19	13·5	0·108	7·41
19·9 ...	18·5–22·0	19	10·3	0·104	9·71
25·0 ...	±1·0	12	7·5	0·0	13·33
30·0 ...	±1·0	13	6·6	0·141	15·15
35·0 ...	±1·0	10	No hatch	—	—

TABLE III.

Length of Larval Period.

Mean temp. °C.	Extreme range of temp. °C.	Initial number of larvae	Final number of larvae	Sex of larvae		Mortality percent.	Mean length of larval period in days	Standard error in days	Percentage development per day
				♂♂	♀♀				
11·7	8·0–14·6	20	13	7	6	35	104·3	5·573	0·96
15·7	13·3–18·0	20	16*	6	4	20	67·2	3·071	1·49
19·6	17·0–21·7	10	10	6	4	—	42·8	1·284	2·34
19·6	17·0–21·7	10	9	5	4	10	42·0	1·457	2·38
25·0	±1·0	20	18	13	5	10	26·5	0·573	3·77
30·0	±1·0	20	11*	4	5	45	25·4	1·050	3·94
30·0	±1·0	20	11*	3	5	45	25·4	0·805	3·94
35·0	±1·0	20	—	—	—	100	—	—	—

* Some larvae died in pupal stage or sex not recorded.

TABLE IV.

Length of Pupal Period

Mean temperature °C.	Extreme range of temperature °C.	Initial number of pupae	Final number of pupae	Mean length of pupal period in days	Standard error in days	Percentage development per day
6·0*	2·4–10·0	11	7	62·4	0·843	1·60
12·0	9·2–14·8	20	17	27·8	0·413	3·60
12·2	9·0–14·8	13	9	28·5	0·562	3·51
15·8	13·6–19·4	21	21	18·7	0·201	5·35
19·2	17·0–21·3	10	9	14·2	0·294	7·04
19·2	17·0–21·3	10	10	14·5	0·320	6·90
25·0	±1·0	20	18	9·5	0·107	10·53
25·0	±1·0	20	18	9·3	0·111	10·75
30·0	±1·0	11	9	9·7	0·199	10·31
30·0	±1·0	10	8	9·7	0·143	10·31

* = Pupae at 6° were at a S.D. of 1 mm.; all others were at a S.D. of 3 mm.

The velocity of development curve has been fitted to the data by the method of least squares. In each case the experimental results at 30°C. have been omitted in calculating the straight line. In the case of the eggs the observations at 30° are not markedly divergent from the straight line, though the total mortality in the experiment at 35° would indicate that 30° must be near the upper limit of the medial temperature range. In the case of the larvae, the divergence of the 30° results from a straight line is more marked and the percentage of mortality is rising. In the case of the pupae at 30° the divergence of the result from the straight line is very marked. The results for the pupae at 6° are also omitted because of the wide fluctuations in temperature around a mean which is near the zero of the velocity curve.

The female larvae tend to have a consistently longer larval life at all temperatures than the male larvae (Table VIII). The sexes are fairly evenly represented in the experimental material except in the experiment at 25°. The curve for the velocity of development of the larvae is based on the results for male and female larvae taken together. There is no indication of any difference in the length of the pupal period of male and female pupae at the same temperature.

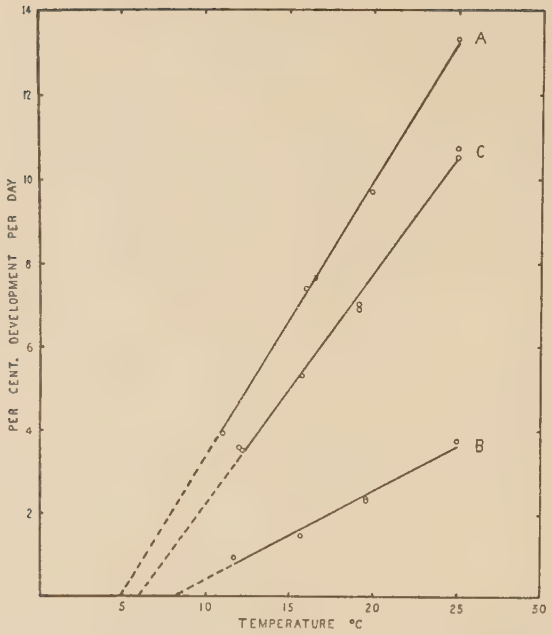

Fig. 1. Velocity of development curves for pre-adult stages of *Tortrix postvittana*. A, eggs; B, larvae; C, pupae.

The calculated values for the straight lines are :—

Eggs :	temperature (t)	=10°C.,	development period (d)	= 29·43 days.
	,, (T)	=20°C.,	,, ,, (D)	= 10·07 ,,
Larvae :	,,	=10°C.,	,, ,,	=240·96 ,,
	,,	=20°C.,	,, ,,	= 39·29 ,,
Pupae :	,,	=10°C.,	,, ,,	= 44·8 ,,
	,,	=20°C.,	,, ,,	= 12·95 ,,

The velocity of development curves are plotted in fig. 1.

The "zero of the velocity curve" (K) is calculated from the formula $K=\frac{d\,t-D\,T}{d-D}$.

The thermal constant (C) is calculated from the formula $C=(T-K)\,D$.

The calculated constants are :—

Eggs :	zero of velocity curve	=4·80°C.,	thermal constant	=153 day degrees
Larvae :	,, ,, ,,	=8·05°C.,	,, ,,	=472 ,, ,, C.
Pupae :	,, ,, ,,	=5·93°C.,	,, ,,	=182 ,, ,,

(*c*) *Interpretation of Field Observations.*

Records of the flight of the adult moth in an orchard at Huonville, Tasmania, during the years 1935, 1936 and 1937, are shown graphically by Evans (Tasm. J. Agric. **8,** no. 3, Suppl., 1937, fig. 4). The dates of maximum abundance of the moths are well defined peaks. Mr. Evans has supplied the mean monthly temperatures for the period in question. These have been used in conjunction with the zero of the velocity curve and the thermal constant for each stage of the insect to calculate the date of maximum abundance of the adults of the different generations. The length of each generation was calculated separately, using as a starting point the observed date of maximum abundance and comparing the calculated peak with the observed peak as a test of the applicability of the constants determined experimentally, to field conditions. The results are shown in Table V.

TABLE V.

Comparison of Calculated and Observed Dates.

Generation	Observed date of maximum abundance of moths	Observed date of maximum abundance of moths of succeeding generation	Calculated date of maximum abundance of moths of succeeding generation
Summer 1935	27/3/35	25/11/35	2/1/36
Winter 1935	25/11/35	29/2/36	24/2/36
Summer 1936	29/2/36	14/11/36	12/12/36
Winter 1936	14/12/36	22/3/37	27/3/37

A slight error may be involved in applying formulae based on experiments at constant temperatures to observations made under variable temperature conditions in the field, since it has been demonstrated for several insects that a variable temperature permits more rapid growth than a constant temperature with the same mean value. The experimental larvae were fed on mature leaves, whereas the larvae in the field show a decided preference for young leaves and develop more rapidly on the latter. The date of the observed maximum abundance of the moths is based on the numbers caught in bait traps and this does not necessarily represent exactly the date of the greatest emergence of moths, since weather conditions following emergence may inhibit flight activity. Considering the sources of error which are involved, the calculated dates approximate very closely to the observed dates, except in the case of the overwintering generation between March and November 1935. The greatest discrepancy between the observed and the calculated dates is to be expected in the case of the overwintering generation, the duration of which is most likely to be affected by factors other than temperature—for example, food and humidity.

2. Larval Instars.

The following experiment was designed to demonstrate the number of larval instars and the duration and width of the head-capsule in each instar. It also provides evidence on the influence of food and sex of the larvae on the number and duration of the instars.

The material consisted of two lots of 20 larvae, all of which were taken from one egg-mass and were therefore the progeny of one female. Both lots were given identical treatment except as to food. One lot was fed on young apple leaves and the other was fed on mature apple leaves. Both lots were given fresh food daily. The individual larvae were isolated in small glass vials stopped with cottonwool and placed in a desiccator in an atmosphere having a saturation deficiency of 3 mm. Hg. Both lots were incubated at 25°C. The time of moulting was known within 12 hours.

The head width—greatest width of the head-capsule—of each instar was measured with a micrometer eyepiece under a monocular microscope. The width was recorded to the nearest unit ; 100 micrometer divisions=0·935 mm. Preliminary comparisons of the width of the head-capsule before and after moulting showed that there was no apparent error in accepting the width of the cast capsule as equivalent to the head width of the larva which cast it. The measurements of all instars were taken on cast capsules, except in the case of the last instar, where it was measured on the living larva before pupation, since the capsule is split on pupation.

(*a*) *Number of Larval Instars.*

TABLE VI.

Number and Length of Larval Instars at 25°C.

Number of larvae	Sex of larvae	Food	Mean length of instar in days						
			1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar	7th instar
8	♂♂	Young apple leaves	7·43	3·87	4·68	6·50	—	—	—
8	♀♀	,,	7·68	3·87	5·31	8·56	—	—	—
1	♀	,,	7·0	4·0	5·0	3·0	8·0	—	—
1*	♀	,,	7·5	1·0	4·5	5·0	8·0	—	—
9	♂♂	Mature apple leaves	7·5	4·1	4·9	7·7	—	—	—
3	♂♂	,,	7·8	3·5	4·6	4·3	7·6	—	—
4	♀♀	,,	7·5	4·3	4·8	4·0	8·5	—	—
1*	♀	,,	7·5	1·0	3·5	4·0	5·0	7·5	—
1*	♂	,,	7·5	1·0	3·5	4·0	4·0	4·0	7·0

* Larvae with abnormally small initial head width.

In Table VI is shown an analysis of the duration of larval instars as affected by sex and food.

The majority of the larvae, consisting of males and females in equal proportions, which were fed on young leaves completed their larval life in 4 instars. The head width of one of the larvae which had five instars was abnormally small in the first instar. Half of the larvae which were fed on mature leaves had more than 4 instars and these included both males and females. The head widths of the two larvae which had 6 and 7 instars were abnormally small in the first instar. The larvae in the field are known to prefer the younger leaves, and the result of this experiment tends to show that the food of the older leaves causes an increase in the number of instars with both male and female larvae.

(*b*) *Duration of Larval Instars and of total Larval Period.*

TABLE VII.

Influence of Sex and Food Quality on length of larval life.

Mean Length of Larval Period in days.

Sex of Larvae	Food	
	Young apple leaves	Mature apple leaves
Male	22·5 (8) ±0·225	25·6(13)±0·668
Female	25·5 (10)±0·229	28·6 (5)±0·111

In Table VII is shown the influence of the sex of the larva and the quality of the food on the total length of larval life at 25°C. and a S.D. of 3 mm. of Hg. The results were tested in pairs for significance, and the following conclusions may be stated :—

1. When male or female larvae at 25°C. are fed on mature apple leaves, the larval period is significantly longer than that of larvae of the same sex fed on young apple leaves.
2. The total larval period of female larvae at 25°C. is significantly longer than that of male larvae with either type of food.

The different rates of development of male and female larvae at 25°C. are also shown in the lengths of the third and fourth instars of four-instar larvae fed on young leaves (Table VI). A similar difference in the rates of development of male and female larvae exists at other temperatures (Table VIII). Separate velocity of development curves for male and female larvae were fitted to the data in Table VIII. The slopes of the two lines are not significantly different. The difference between the velocity values for male and female larvae at the mean temperature approaches significance.

TABLE VIII.

Influence of Sex on Length of total Larval Period.

Mean temperature °C.	Length of total larval period					
	Male			Female		
	Number of larvae	Mean length in days	Standard error in days	Number of larvae	Mean length in days	Standard error in days
11·7	7	91·8	4·691	6	118·8	13·292
15·7	6	58·8	2·116	4	64·0	2·943
19·6	6	40·8	1·435	4	45·7	1·518
19·6	5	39·4	1·680	4	45·2	1·270
25·0	13	25·6	0·668	5	28·6	0·187
30·0	7	23·0	0·634	10	27·6	0·434

(*c*) *Head Width of Larval Instars.*

Table IX is an analysis of the head widths of the larval instars. The measurements are derived from the larvae which furnished the material for Table VI.

TABLE IX.

Head Width of Larval Instars.

Number	Sex	Food	Mean head width in micrometer divisions						
			1st instar	2nd instar	3rd instar	4th instar	5th instar	6th instar	7th instar
8	♂♂	Young leaves	33·3	52·2	81·5	119·7	—	—	—
8	♀♀	,, ,,	34·0	54·7	87·2	130·3	—	—	—
1	♀	,, ,,	33	49	—	95	135	—	—
1	♀	,, ,,	22	35	54	88	132	—	—
9	♂♂	Old leaves	34·1	51·1	81·2	122·0	—	—	—
3	♂♂	,, ,,	33·0	47·6	72·0	95·6	127·6	—	—
4	♀♀	,, ,,	33·2	50·0	74·0	99·7	134·5	—	—
1	♀	,, ,,	23	34	48	72	99	137	—
1	♂	,, ,,	23	33	35	49	71	92	123

Food quality has no apparent influence on the head width of the final instar of male or of female larvae.

The mean head width of the last instar of 8 male larvae with four instars was 119·7±0·758 divisions and that of 8 female larvae was 130·3±1·261 divisions. The head width of the final instar of four-instar female larvae is therefore significantly greater than that of four-instar male larvae when both sexes are fed on young leaves. The same tendency is evident in the second and third instars also (Table IX).

Although the larvae were all from the same egg-mass, the initial head widths of three of them were much smaller than the others and these three larvae had one more moult than the greatest number of moults undergone by larvae of normal initial size.

(*d*) *Determination of Instars of Larvae of unknown Age.*

The range of head widths of larvae with four and five instars is shown in Table X.

TABLE X.

Range of Head Widths of Larval Instars.

25 Larvae with 4 instars			7 Larvae with 5 instars		
Actual instar	Range of head width		Actual instar	Range of head width	
	Micrometer divisions	mm.		Micrometer divisions	mm.
I	32–35	0·299–0·327	I	32–34	0·299–0·317
II	48–56	0·448–0·524	II	46–52	0·430–0·486
III	75–90	0·701–0·841	III	66–79	0·617–0·738
IV	116–135	1·085–1·262	IV	92–102	0·860–0·954
			V	126–136	1·178–1·272

If the samples are sufficiently large to give a reliable measure of the range of variation in head width within each instar, it is evident that (excluding the small percentage of larvae which were initially of abnormally small head width) larvae in the first, second and last instars may be determined with a fair degree of certainty. The separation of the third instar of four-instar forms from the third and fourth of five-instar forms could not be done with any certainty.

It is possible that for some experimental purposes the response of the larva is a function of its size irrespective of the instar (except possibly in the case of the last instar) and for such purposes the head width might be used as an objective index of size.

3. Factors in Larval Mortality.

A few experiments were made on the rate of mortality of (*a*) larvae subjected to high temperatures and (*b*) larvae subjected to starvation at low temperatures.

The larvae were isolated in glass tubes stopped with cottonwool. At high temperatures the larvae were placed in desiccators containing the appropriate solution for the control of humidity, in a Hearson incubator. At the low temperatures the tubes containing the larvae were placed in glass jars over the appropriate salt solution, in the multiple temperature incubator. They were examined daily and in the case of the larvae at high temperature they were fed daily on mature apple leaves.

(*a*) *High Temperature.*

Two experiments were made. Each consisted of 20 larvae which were incubated at 35°C. and a saturation deficiency of 3 mm. of Hg. One lot consisted of first instar larvae and the other was a mixed lot of second and third instar larvae. The mortality curves are shown in fig. 2. The 50 per cent. mortality point is lower than in the case of starved first instar larvae at low temperatures, but this may be partly due to the higher S.D. (3 mm.) and not entirely an acceleration (as compared with the mortality due to simple starvation) due to the lethal action of high temperature. It is noticeable that the larvae feed very little after a few days have elapsed. The larvae in the older lot frequently showed strings of tissue attached to the excreta before death occurred.

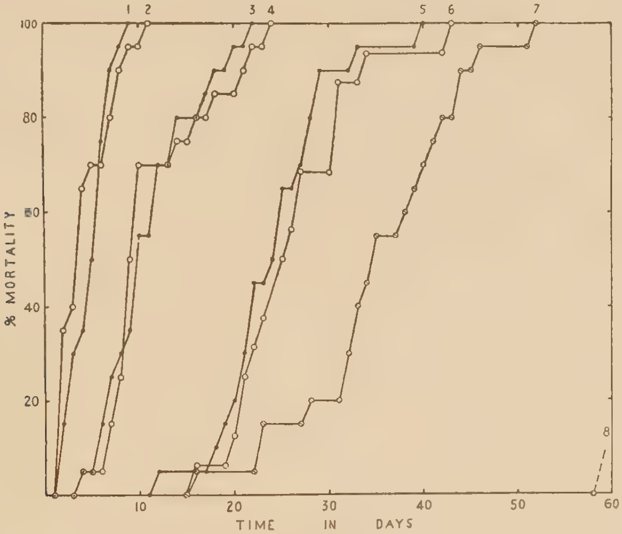

Fig. 2. Rate-of-mortality curves for larvae of *Tortrix postvittana*.

(*b*) *Starvation at Low Temperature.*

The results are shown in fig. 2 and Table XI.

TABLE XI.

Mortality of Larvae.

Experiment No.	Number of larvae	Stage of larvae	Food conditions	Mean temp. °C.	Relative humidity per cent.	Saturation deficiency mm. Hg.	50 per cent mortality point days	Mean head width of larvae†
1	20	II & III	Fed	35	92·5	3	5·0	33
2	20	I	,,	35	92·5	3	3·3	33
3	20	I	Starved	5·3	97	0–1	9·7	33
4	20	I	,, *	5·3	97	0–1	9·0	33
5	20	II	,,	5·4	54	3	24	49
6	16	IV & V	,,	15·9	92·5	1	25	112
7	20	II & III	,,	4·6	97	0–1	34·4	65
8	17	Last	,,	5·5	97	0–1	59†	125

* Newly hatched larvae, unfed. † In micrometer divisions.

In the experiment with last instar larvae eleven had pupated after 41 days and none had died. Of the remaining six, two died after 59 days and a third after 60 days. Three surviving larvae, after 73 days, were given food and incubated at 25°C. and all pupated. All six larvae while at low temperatures had attempted to feed on the cottonwool plugs. The temperature was evidently not sufficiently low to inhibit feeding.

The mortality curves are typically sigmoid. The results of experiments 3, 4, 5, 7 and 8, which were carried out under comparable conditions of low temperature and high humidity, show a tendency for the survival time to increase with the increase in size of the larvae. The larvae in experiment 5 were subjected to a greater S.D. and the results may therefore show an adverse effect of low humidity. The low result in experiment 6 is presumably due to an acceleration of mortality caused by the higher temperature.

The indications are that last-stage larvae under conditions of low temperature and high humidity are able to survive in the absence of food for periods up to 2½ months. These results are similar to those of Evans. Under the conditions of these experiments there were indications that the desire to feed was not entirely inhibited. The winter temperatures in the field would not remain consistently as low as those used in this experiment and it is probable that the larvae would have the urge to feed and would do so if food were available. If the larvae overwinter in the orchard, they could feed on the buds or green bark of the apple trees (as related species are known to do) or else on weeds or cover crops in the orchard. There is no evidence that a significant proportion of the larvae winter on the tree, while Evans has produced evidence indicating an invasion of the tree by larvae in the spring, under Tasmanian conditions. Starved larvae could survive for a period of two months or more, but there is no evidence that the larvae enter a temperature-governed hibernation. It is likely, therefore, that the larvae which overwinter within the orchard feed on weeds or cover crops.

Acknowledgments.

I am much indebted to Dr. J. Davidson and his colleagues of the Entomology Department of the Waite Institute at Adelaide for helpful criticism and assistance ; to Miss H. M. Brookes for attention to experiments in the writer's absence ; to Mr. J. W. Evans, Government Entomologist, Hobart, for supplying experimental material and meteorological data ; and to Miss F. E. Allen of the C.S.I.R., Canberra, for assistance with the statistical interpretation of some of the data.

Summary.

1. The thermal constant and the zero of the velocity curve have been determined for each of the pre-adult stages of *Tortrix postvittana*, Walk. The experimental methods are described. The thermal constant for the eggs is 153 day degrees C. and the zero of the velocity curve 4·80°C. The corresponding constants for the larvae are 469 day degrees C. and 8·05°C., and for the pupae 182 day degrees C. and 5·93°C.

2. The experimentally determined constants and the mean monthly temperatures have been used to calculate the peak of the flight period of the adult moths at Huonville, Tasmania, during the 1935, 1936 and 1937 seasons. In three cases out of four the calculated dates approximate very closely to the observed dates for the peak of the flight period.

3. The results of observations on the number, duration and head-widths of the larval instars are given. The majority of larvae fed on young apple leaves had four instars. A greater proportion of the larvae fed on mature apple leaves had more than four instars. The length of larval life at 25°C. is significantly longer for both male and female larvae when they are fed on mature leaves. The head width of the final instar of four-instar female larvae is significantly greater than that of the final

instar of four-instar male larvae. Food quality has no apparent influence on the head width of the final instar of either male or female larvae.

4. At 25°C. the length of larval life of female larvae is significantly longer than that of male larvae when both are fed on the same food; the same tendency is exhibited at other temperatures. The separate velocity curves for male and female larvae are not significantly different in slope. The difference between velocity values for male and female larvae at the mean temperature approaches significance.

5. Larval mortality increases rapidly at temperatures above 30°C., and 100 per cent. mortality occurs at 35°C. Starved larvae at low temperatures and high humidities show a tendency for the survival time to increase with the size of the larvae. Final instar larvae under these conditions can survive for two and a half months.

INVESTIGATIONS ON THE COTTON BOLLWORM, *HELIOTHIS ARMIGERA*, HUBN. (*OBSOLETA*, FABR.)*

Part I.—The Annual March of Bollworm Incidence and Related Factors.

By F. S. Parsons, B.Sc.Agr., F.R.E.S.

(Plate X).

Introduction.

In a previous paper (Parsons & Ullyett[1]), an account was given, for the period 1929–32, of methods of field and laboratory surveys of a continuous and quantitative nature which had been designed for enlightenment on the annual course of bollworm breeding and particularly on factors conditioning the time and character of bollworm incidence in rain-grown cotton. The need for precise information in these regards was an imperative preliminary to the conduct of field experiments on the value of the egg parasite, *Trichogramma luteum*, Gir., to which, as indicated in a later publication (Parsons & Ullyett[2]), attention was devoted practically from the inception of work at Barberton on the control of cotton pests. Apart from immediate application to the problems of evaluating parasite intervention, the fullest information on the incidence, habits and reactions of the bollworm was required before attempting any other measures for evasion or control of bollworm attack in the cotton crop. This information has been sought in data obtained during the past nine years by the system of survey as described in 1934 and since improved. In consequence the bollworm problem is now understood in many particulars, and measures for alleviating the bollworm menace in cotton-growing have been indicated and tested with considerable success.

It was realised early that the bollworm situation in cotton, season to season, would depend very largely on influences exerted by other food-crops of the insect, grown prior to and in conjunction with cotton, and that, therefore, observations should extend over the whole range of wild and cultivated food-plants as found to be attacked in the course of the year. Knowledge of the train of events leading to the appearance of the bollworm in cotton and the part played by alternative food-crops associated with cotton is a logical and necessary prelude to field work on bollworm control, and a discussion of extended views on the various factors involved have been presented by the author elsewhere[3] and have been reiterated in the Annual Reports from the Cotton Experiment Station, Barberton[4]; further discussions will, however, be appropriate when dealing specifically with subjects raised in this and later communications.

The present paper treats of recurring phenomena which form the background of our present-day concept of the problems and of the investigations devoted to them.

Methods.

The course of oviposition as determined throughout the year by counts of eggs per plant in sampled areas of all types of food-plant is our criterion of moth incidence. As explained in the reference[1], it has been possible to obtain accurate records on the necessarily extensive scale by utilizing native recorders under European supervision.

For calculations on an acceptable basis of egg and larval populations per unit-area and per crop-area, it was essential to evolve a satisfactory technique of sampling.

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* Contribution from the Cotton Insect Pest Control Department of the Cotton Experiment Station, Barberton, South Africa.

This presented uncommon difficulties because moths in egg-laying discriminate with respect to the stage of development of the food-plant as well as to small differences in its health and environment, hence methods devised for plants only are not applicable directly. Prior to 1934 it was questionable if our sampling procedure was valid for present purposes, and for that reason data from the earlier years of work are not included in this discussion. In 1934, however, the author's colleague, Mr. Joseph Marshall, collated data from precision experiments, similar in design to that employed by Kalamkar[6], in order to investigate the nature and form of distribution of the egg-laying by *Heliothis armigera*. Marshall found that the degree of asymmetry exhibited by the data from grouped sample units did not preclude use of the statistics applicable to the normal curve and, following a series of sampling tests, he was able to devise a technique of the required standard of efficiency, the particulars of which have been reported[5]. This constitutes the principal alteration in the field methods outlined with results to 1932[1, 2], and imparts a higher standard of value to all aspects of the work subsequently undertaken.

Character of the Seasons and Food-plant Situations.

De Kaap Area of the Eastern Transvaal.

The warmer, rainy months of the year are embraced in the period October to May, inclusive. The temperature falls in May and cool, dry weather is experienced until September ; mean weekly temperatures of the air under standard screen conditions are depicted in fig. 1. There is great variability in the distribution and volume of the rainfall, and planting dates, season to season, range widely from October onwards. Cotton, which has a long-growing habit, is planted with the earliest suitable rains, and other summer crops may be set out simultaneously with cotton or in one or more later plantings, and as circumstances permit, within the first two to three months of the rainy season. Harvesting of the summer crops is completed in the cool season and non-irrigable lands are then, as a rule, left untouched until prepared for seeding after the commencement of the rains ; dry ploughing is practised but little.

On farms with irrigation facilities, and this applies particularly to the environs of Barberton where the Cotton Pest Survey has been most highly developed, vegetable and orchard crops are produced in quantity from July to November, but particularly during August, September and October. The higher temperatures in October and November hasten ripening processes but increase the spoiling of produce in the fields and during shipment so extensively that field crops of this nature are always discontinued in November.

There are then two main periods of cropping, viz., the rain-grown or summer season which lies between October and May, and the irrigated or winter season which lies between July and November. In both cases growth and fruiting are at their maxima about midway in the periods.

If October rains are suitable for planting, very young rain-grown crops are co-existent with the ageing irrigated crops of the vegetable character. More often there is a definite interval between the purely winter- and summer-cropping periods, and, if the rains are very late, this may extend to several weeks. Irrigation is used, however, to promote and, if need be, maintain relatively small areas of tobacco and maize in growth during November and December. These constitute crops intermediate between the two main phases of agriculture. Additionally, at this time weed growth in the irrigated lands is profuse, as it also is to a lesser extent, given even light rains, in ploughed and unploughed dry lands ; from time to time ratooned and standover cotton have also contributed to the food-plant situation in November and December.

From May to July cultivated food-plants of the bollworm are furnished principally by a little fodder maize, occasional cotton and bean crops and volunteer crop plants ; natural food-plants are present to some extent. There is thus continuity throughout the year, though in greatly differing quantities, in the supply of known food-plants of *Heliothis armigera*.

To the north of Barberton and beyond a barrier of hills are large tracts of citrus orchards intermingled in the cool season with vegetable crops. Eastward along the valley of the De Kaap River and connecting with the eastern extremity of the Barberton terrain are other large sections of winter-grown vegetables and fairly extensive citrus orchards. In these outlying districts rain-grown crops are at a minimum and, as noted later, the circumstances of bollworm incidence were surveyed for two years with particular reference to possibilities of moths migrating thence into the rain season crops within the compass of the intensive survey near Barberton.

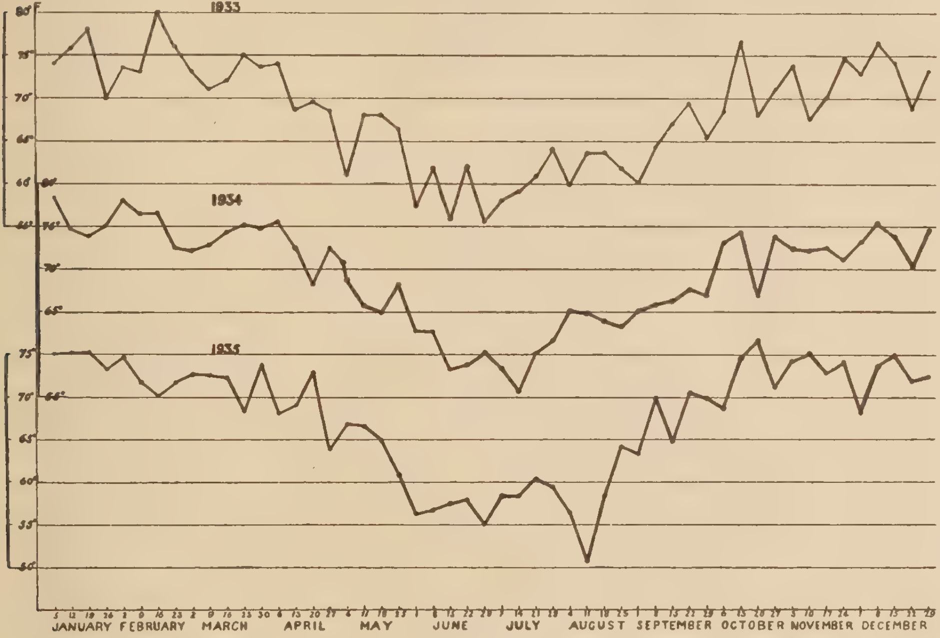

Fig. 1. Mean weekly temperatures of the air.

Swaziland and Natal.

The methods of survey have been applied to a considerable degree in the cotton-growing areas of Swaziland and Northern Natal. The rainy season in these areas is also highly irregular ; it differs from district to district and within districts there is frequently no accord in dates of planting crops dependent on rainfall moisture only. The physiography of the country (including in part the Eastern Transvaal) has been discussed and mapped previously (Marshall, Parsons & Hutchinson)[7]. Temperature distinctions may be drawn between the regions at various altitudes, but the more important aspects are contained in the food-crop situations, as follow.

Practically speaking there are no winter-irrigated crops in the cotton-growing areas of Swaziland, and bollworm breeding in the cool season, and until rain-grown crops are invaded, is confined very largely to natural food-plants, which are not abundant until the rains occur. In the Pongola-Magut area of Natal there are extensive irrigation projects where the tendency is for continuous cropping. In juxtaposition to these are dry farming sections susceptible to invasion in the rainy season by bollworm moths propagated in the irrigated food-crops.

In the earlier years of the Survey, information on the course of bollworm behaviour in other cotton-growing areas of the Transvaal and in neighbouring portions of Portuguese East Africa was obtained through an intelligence service founded in co-operation with the managment of large cotton estates. The supply of information terminated upon discontinuance of cotton-growing with the fall in prices of raw cotton, but in retrospect is found to supplement data obtained over a longer range at Barberton, in Swaziland and Natal.

In all the areas surveyed, the phenological aspects of bollworm incidence agree closely as regards the summer season when cotton is grown. Presentation, as in the following, of the evidence obtained at Barberton alone will serve, therefore, to illustrate this. Differences between areas in the train of antecedent events are more questions of the scale of bollworm breeding at any one period than of interruption in the sequence of events, and these are discussed in the text where needful.

Bollworm Incidence.

Taylor,[8] working at Barberton prior to 1929, observed that *H. armigera* was present throughout the year, and there are references in South African literature to the same effect regarding other areas of corresponding altitude in the Transvaal. In a reconnaissance by the author (1929–30) large quantities of the bollworm eggs and larvae were found except during May, June and July, when very few were evident.

Apart from the cultivated field and orchard crops which have their limited seasons of growth, the reconnaissance covered a wide range of natural food-plants, particularly those occurring between the main cropping periods, *i.e.* May to July and during December, and thus insured continuity of records ; in the reconnaissance the mere presence or absence of bollworm was noted. On most occasions eggs and larvae were to be found on several species of food-plant ; areas of food-plants in various stages of growth were present and, there being then no information on the habits of the moth in relation to the plant, it was necessary to conduct searches for evidence of bollworm activity over the whole range of the food-plant assemblies existing at any one time. It appeared improbable that a food-plant complex embracing all the variables throughout the year would develop in any one instance in the dual irrigation and dry farming enterprises, since that would depend on climatic vagaries, the intentions of the farmer and other factors. Perforce of these considerations and using the new methods devised for the quantitative survey of bollworm incidence, the field crop and orchard-bearing portions of seven farms lying in a triangle of about twenty-five square miles adjacent to Barberton were utilized for the accumulation of comprehensive records ; instances of solely dry farming and admixtures of irrigation and dry farming practices were well represented, with the accompanying combinations of natural food-plants in cultivated and uncultivated lands and woodland areas.

Briefly the primary objectives were, firstly, to lay bare the true course of bollworm breeding through the year and, as a corollary, the principal sources of moths entering cotton and other summer crops—this with a view, then, to the application of control measures at source. Secondly, repeated observations were desired over a wide field to determine the relationship of the moth with individual species of food-plant, as evidenced by the course of oviposition ; observation of the growth condition of the plant being inseparable from this. Thirdly, although something was known or surmised of preferences exhibited by the moth for certain species of plant, the subject demanded much more extensive enquiry, especially before attempting to exploit any such relationship.

The extent of the survey as applied originally was born of the effort to avoid *lacunae* in the records due not to diminished populations of moths but to overlooking of food-plant units where egg-laying might be in progress. Experience disclosed, however, that for most purposes the area of operations could be much reduced without loss of information. Since 1933 the data used in the present paper have been drawn from smaller but comprehensive examples of food-plant situations. These, in which the Cotton Experiment Station represents the summer crop phase, allow of sufficient overlap in the progression of crops and colonies of naturally-occurring plants *attractive* to the moth to obviate misinterpretation of moth prevalence. The word attractive is emphasized, as it was established early that the moth oviposits on all its food-plants common to the region only when they are in bud and flower.* This finding has simplified greatly the task of recording and has proved a most reliable and valuable guide in the pursuit of information on moth activity and has shown that it was but wasted effort to examine crops for eggs before and after the budding and flowering stages of a food-plant.

The graphs in fig. 2 depict the course of oviposition on field crops continuously from June 1933 to May 1938. The points plotted represent the total eggs estimated to be present at each date of record on the whole of the cultivated crop section of the area under survey in this connection ; orchard and natural food-plant records are not included, as explained presently. In computing the totals, egg counts, as taken on the sample units in each type of crop, have been raised to eggs-per-crop-area by using factors for multiplication appropriate to the size of units and the inter- and intra-row spacing of plants and after excepting measured portions of backward or poorly-grown crops unvisited by the moth (habitually the moth confines oviposition to the healthiest, best-developed, and most freely-flowering portions). Various types of crop which experience very different rates of egg-laying are thus considered individually and in the aggregate on the basis of acreage, and due importance is attached to occasions, for instance, of light egg-laying per plant but over large bodies of crop, or of concentrated laying on small bodies of a food-plant favoured by the moth and other similar occurrences.

The validity of the measures taken to obtain the collective figures illustrated in fig. 2 rests largely upon Marshall's work on sampling procedure (*l. c.*), as adopted here. Investigations have shown that the sampling error is not unduly high except when very light oviposition obtains. It may be assumed that the eggs present are generally under-estimated, but the objectives are attained if the picture obtained agrees in the main features with actual conditions. That it does so in the directions of revealing moth preferences in the choice of food-plants and the stability of the oviposition-flowering association will be demonstrated amply in later communications. With regard to the annual march of bollworm incidence, as shown by oviposition, attention is now drawn to fig. 2.

The events graphed in fig. 2 may be divided into five periods which are fairly well common for each of the five years. Two periods of low activity are shown, May, June and July, and the month of December, with, in 1936, extension through January. As presented in the figure, these two periods are not altogether true reflections of moth prevalence for the following reasons. It may be recalled that small areas of maize, tobacco and, occasionally, ratooned and stand-over cotton, constitute the crops in growth during late November and December ; various sections of them are then in flower and attract the egg-laying moths. The data given in each case for December are from records on these crops only, and as it is customary to deflower tobacco plants, emphasis may be placed on the others. Coincidentally, however, extensive oviposition is taking place on flowering weeds, principally †*Datura stramonium*, L. (=*D. tatula*, L.), *Nicandra physaloides*, Gaertn., *Malvastrum*

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* Known exceptions to the rule are the chick pea, *Cicer arietinum*, and a variety of the hyacinth bean, *Dolichos lablab*, both recently introduced into the area. Furthermore, in the absence of flowering food-plants, eggs may be found occasionally on non-flowering crops.

† Formerly it appeared from oviposition records that *Physalis angulata*, L., was of outstanding importance. The eggs deposited on this plant are indistinguishable from those of *H. armigera* but were found to be laid by *Heliothis assulta*. *P. angulata* is the only important food-plant of *H. assulta* that we have encountered.

tricuspidatum, A. Gray, *Sonchus oleraceus*, L., *Xanthium pungens*, Willd., and *Sida* spp., all of which are to be found in great but widely scattered quantities throughout the countryside. A list of the natural food-plants recorded is supplied in Appendix I, and attention is invited to those of particular importance in fostering bollworm in Swaziland prior to the rains. Except in particular instances it is not possible to estimate on an acreage basis the undoubtedly high numbers of eggs deposited on these plants and no indication of them can be given in fig. 2. Actually a peak of laying occurs in December which is of first importance with regard to the early infestation of rain-grown cotton, and the subject is reverted to in the succeeding section on the origin of moths.

The principal explanation of the low activity exhibited for May, June and July, lies in the fact that a high proportion of the larvae pupating in April and May enter

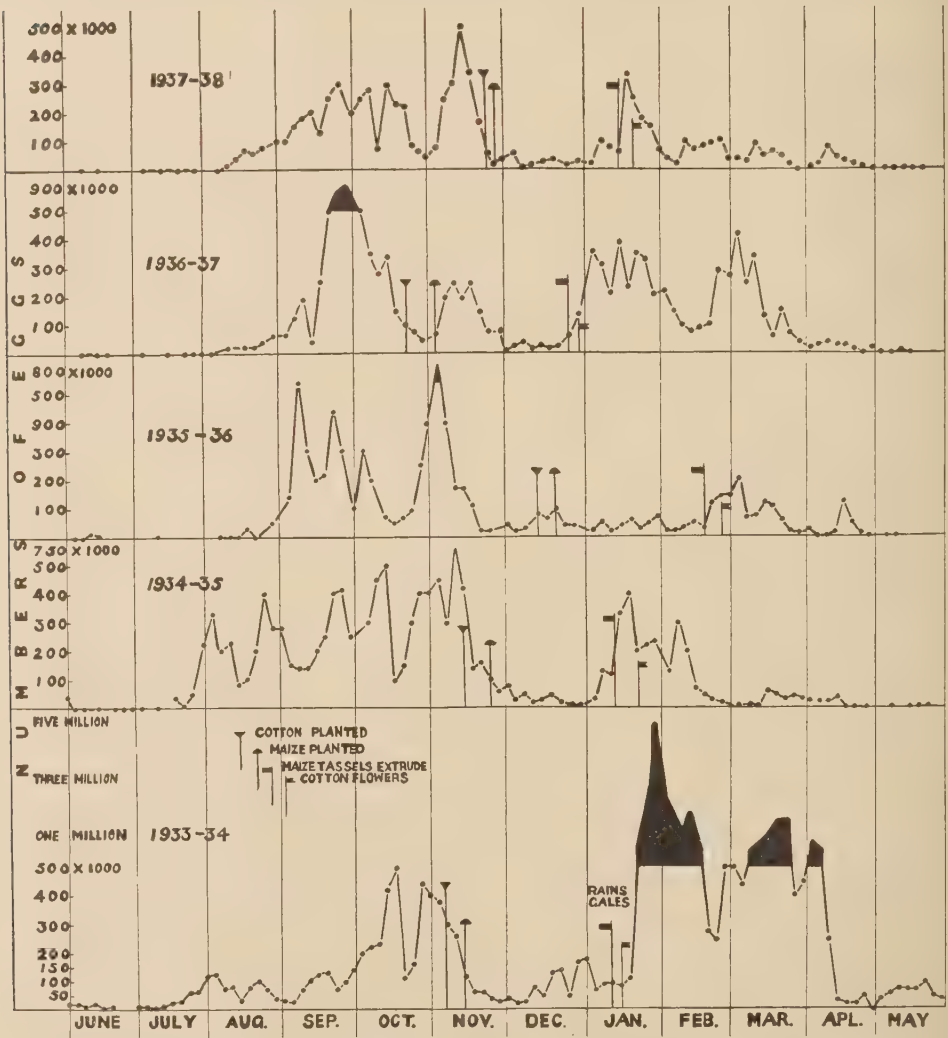

Fig. 2. Graphs depicting the course of oviposition on field crops continuously from June 1933 to May 1938.

a diapause extending beyond July. The course of moth emergence from these, the last considerable pupations at the close of the summer season, is given for three years in fig. 3 where it will be seen that 65 to 85 per cent. of the emergence takes place after July. Emergence is relatively slight in June and July but varies from about 8 to 15 per cent. in May. These percentage proportions are based on relatively small samples from variable larval populations, and the actual number of moths in flight, particularly during May, are probably more considerable than the data in fig. 2 indicate, and this is borne out to some extent by information obtained on moth

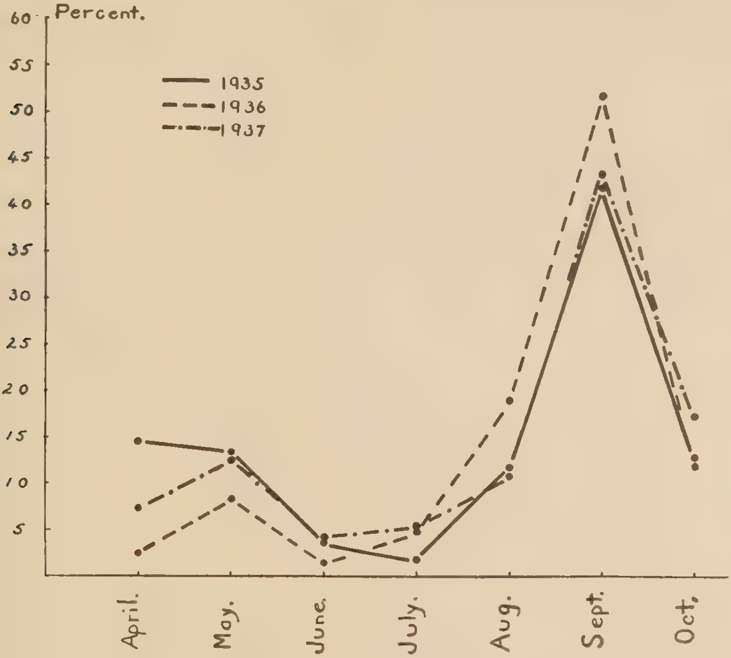

Fig. 3. Moth emergence from pupae—diapause.

flights, as displayed later in fig. 5. Other factors concerned in May and June, however, are as follows :—Summer crops are senescent in May, and such small patches of very late-planted or volunteer crops as there may be grow poorly at the lower temperatures, flower sparsely and receive little egg-laying ; as in the December instance, records are confined to these. On the other hand, natural food-plants are at a minimum, restricted by climate, and generally out of flower. In the comparative absence of floral nectaries it follows that food for the moth, an essential pre-requisite to fertilization, is scarcely obtainable at the main source ; probably, therefore, the situation for May, June and July is not greatly under-estimated. Only moths from a portion of the April and early May larvae can participate, as the minimum pupal period for many April, most of the May and all of the June and July bred larvae does not permit emergence until August. The bollworm is definitely least active in these months and, as they mark an interval imposed by climate and persistent farming practices between summer and winter crops, it is convenient, as represented in fig. 2, to consider the " Bollworm Year " as lying between 1st June and 31st May.

The active period, August to November inclusive, is apparently one of major incidence, although considerable fluctuations are evident in four out of the five cases illustrated. Many of the instances of low laying are associated, however, with winds of gale force and dust storms characteristic of the dry season, or light rains inhibiting oviposition, occasionally hailstorms ; some connection is also traceable with moonlit periods. Uninfluenced by these the oviposition which is due in the first instance to moths emerging from diapause, and which falls almost entirely on vegetable and orchard crops, would certainly have followed a less irregular course, rising to more definite peaks in September and October, as for example in 1936.

The time of the onset of oviposition on winter crops differs somewhat, being related to the varying influence of soil temperature and moisture on the pupal phase, a subject under investigation. In fig. 2 there are, however, two obvious periods of high laying between August and late November. The peak falling in late October to some time in November is common to each year, and its recurrence is a prominent feature of the data.

The graphs for four of the five years suggest that the winter crop season is one of transcending bollworm activity. If to this the oviposition on citrus (of which there are relatively large acreages) be added, the September–October figures would be enhanced very greatly ; but it has not been possible to devise a satisfactory method for determining the weight of egg-laying on citrus trees. It has sufficed to be aware that eggs are laid on citrus coincidently with the blossoming (firstly of the navel orange trees, followed about 10–14 days later by trees of the Valencia variety) which occurs commonly some time in September or October. In our problems of bollworm control a somewhat false (as events reveal) importance has attached to the relative status of winter and summer infestations, and the subject has been investigated extensively. It has been difficult to appraise the position numerically in the Barberton area owing to the contiguity of solely winter crop situations lying eastward, but deduced from particulars of crop and orchard acreage, coupled with periodic egg counts taken widely and specifically from Barberton, it appears that moth activity in the cool season does predominate. The subject has been examined, however, more reliably on an isolated estate in Natal, where a fitting basis for comparison was to be found with little danger of moth influx from outside sources of breeding ; the findings substantiated the impressions gained at Barberton.

TABLE I.

Periods in Days from Planting to Peak of Tasselling of Five Varieties of Maize grown under varying Conditions. 1932–1935.

Dates of planting	Soil type	Days to peak of tasselling				
		Varieties				
		Flint	Hickory	Peruvian	P. Pearl	Anveld
19.xii.32 ...	Red loam	64	67	59	69	—
23.i.33... ...	,, ,,	62	67	61	70	63
17.xi.33 ...	,, ,,	67	72	—	76	66
4.xii.33 ...	,, ,,	66	68	64	71	66
3.i.34... ...	,, ,,	66	66	59	74	59
22.xi.34 ...	,, ,,	69	71	65	77	67
11.xii.34 ...	,, ,,	67	68	65	74	65
7.i.35	,, ,,	66	70	63	71	64
20.xii.32 ...	Granite ...	60	64	59	—	—
23.i.33... ...	,, ...	63	66	61	—	—
4.xii.33 ...	,, ...	67	69	63	72	66
5.i.34... ...	,, ...	66	66	62	72	64
12.xii.34 ...	,, ...	69	74	69	79	69
3.i.35... ...	,, ...	63	65	62	—	62
10.xii.35 ...	,, ...	63	68	—	—	62
	Mean ...	65	68	62	73	64

The other main period of activity displayed in fig. 2 falls in the rainy season between the end of December and the end of April. As stated previously records taken on the Cotton Experiment Station only have been utilized in the portrayal of the summer incidence.

As *Heliothis armigera* practically confines oviposition to plants advanced in bud and in flower, the discussion of bollworm incidence on rain-grown crops resolves largely into considerations of when crops have been planted and when they become attractive to the egg-laying moth ; it should be apprehended that whilst the rain crops proper are in the pre-flowering condition moth activity is exhibited over the maize, tobacco and natural food-plants referred to in the remarks on the December period.

Eighty to ninety per cent. of the rain crops consist of cotton and maize. Eggs are not deposited on maize in quantity until extrusion of the tassels occurs (Parsons & Ullyett[1]). The interval of time from planting to the peak of tasselling of each of the varieties grown does not vary by more than a few days, season to season, regardless of growing conditions. The evidence on this point is submitted in Table I.

The figures in Table I have been obtained from Mr. M. F. Rose, in charge of rotation crop work at Barberton. Latterly, following selection in the Flint and Hickory varieties, the period has become regularly 58–60 and 60–64 days respectively. A selection from Anveld (due to Dr. Saunders of Potchefstroom), first grown in 1938, comes into general tassel about 51 days from seeding.

In all the varieties grown tassels extrude and the maize crop becomes attractive to moths for oviposition about twelve days prior to the peak conditions on which the times in Table I are calculated.

Heliothis eggs occur on budding cotton to some extent, but major layings are associated always with flowering. The interval between planting and the appearance of the first flower for several strains of the U.4 cotton grown here has varied only from 66 to 72 days in three years' observations.

The earlier dates of planting maize and cotton are indicated in fig. 2. Opposite these are marked points representing the commencement of tassel extrusion, according to the variety concerned, and the occurrence of first flowers in cotton, taking the period from seeding to flowering in cotton to be 68 days for all years. For convenience the dates concerned are assembled below :—

Maize	Planted	Tassels appear	Cotton	Planted	Flowers appear
1933–34 ...	14.xi.33	8.i.34	1933–34 ...	6.xi.33	13.i.34
1934–35 ...	20.xi.34	13.i.35	1934–35 ...	13.xi.34	20.i.35
1935–36 ...	22.xii.35	14.ii.36	1935–36 ...	21.xii.35	27.ii.36
1936–37 ...	3.xi.36	23.xii.36	1936–37 ...	20.x.36	27.xii.36
1937–38 ...	26.xi.37	13.i.38	1937–38 ...	23.xi.37	20.i.38

Apart from a minor rise in early January 1938, due to oviposition on *Dolichos lablab* (an exception, as noted to the oviposition-flowering relationship), and non-conformity in the first half of January 1934, due to inhibition of egg-laying by rains and gales, there is seen in fig. 2 to be a very close coincidence between the rise of egg numbers and tassel extrusion in maize.

Maize is a preferred host and commonly receives a high preponderance of the egg-laying. Based on this and the constancy of the periods, seeding to flowering, of both cotton and maize, opportunity has for long been taken to test the utility of maize in diverting moths from cotton. Maize is attractive only for about fifteen days,

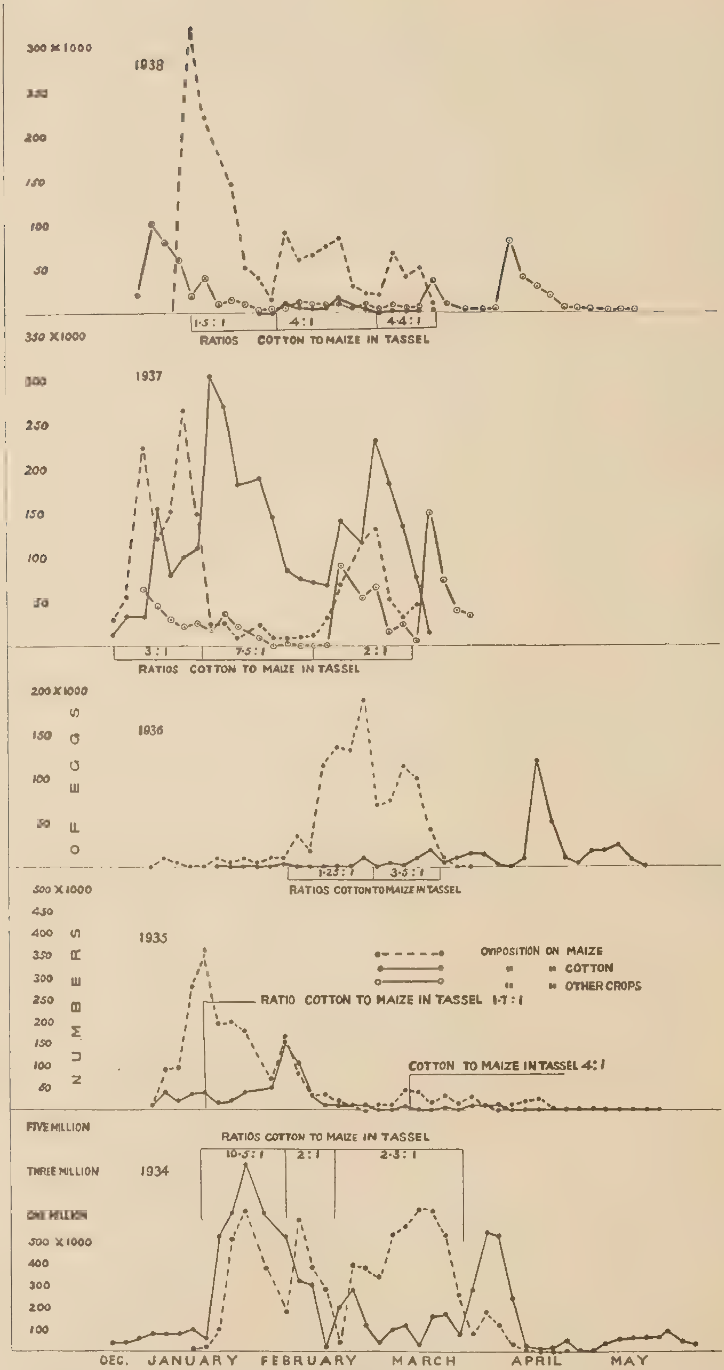

Fig. 4. Relative oviposition on summer crops and ratios of the acreages of cotton to maize.

and its ampler use for diversion purposes entails two to three successive plantings in order to span the January–February period of high laying ; the diversion of moths to maize so interposed results in freeing cotton from much bollworm loss amongst the early-set fruit, fruit which contributes a large proportion of the crop yield. Apart from 1934, the ratio of early maize in tassel to cotton has been high, and the figures for the January–February oviposition derive mainly from eggs laid on maize. *Inter alia* the value of maize as a counter-attractive crop has been demonstrated fully elsewhere in the Barberton area, in Swaziland and Natal, and doubts on the grounds, widely entertained, that it has a high breeding propensity, ultimately resulting in heavier attacks on cotton, have been dispelled following studies on comparative larval mortality.

Successive oviposition on the summer crops falls partly on late maize, more on cotton as maize protection lessens, and partly on small bodies of groundnuts, sorghum, sunn hemp, chick peas and *Dolichos*. It will clarify the situation to illustrate, as in fig. 4, the relative oviposition on the summer crops for the five years ; this figure also contains particulars of the ratios in acreage of cotton to maize.

The mean period from egg to egg-laying moth again is 42 days in January and February, increasing to 47 and 51 days in March and April in cases where the diapause does not obtain. Theoretically crops planted in October and November are liable to experience four to five generations of bollworm. Applying the data on the developmental period of the insect, as above, from the onset of oviposition on summer crops in December, January, or February, as the case may be, little agreement can be found in fig. 2 between the theoretical and the observed course of events, especially as regards the times of occurrence ; there are also questions as to the diminishing activity observed. Explanations of these discrepancies and reduced populations rest on analyses of contributing factors which form the subjects of later communications ; conformably discussion on differences in the status of successive summer and winter infestations is also deferred.

From the evidence obtained in the survey, of which the data in fig. 2 supply a concrete example, it may be stated that marked periodicity is implicit in the march of bollworm incidence year to year ; a time sequence is apparent, dividing the year into five periods, which briefly in review are as follows :—

1. *May, June and July.*

Bollworm is least active, restricted by food and climatic factors ; pupae are diapausing. Harvesting of rain-grown crops is in progress, irrigated crops are scarcely advanced beyond the seedling stage. All things considered, it is appropriate and convenient to regard the " Bollworm Year " as from 1st June to 31st May.

2. *August, September and part October.*

Recrudescence of bollworm activity is incepted as break-up of dormancy commences. The infestation gains magnitude as moth emergence increases. The insect is fostered on abundant irrigated crops, and exceptionally heavy incidence is witnessed during this and the succeeding period. Oviposition on citrus is not included in fig. 2.

3. *Part October and November.*

A peak of activity distinct from the foregoing occurs on irrigated crops. This, it may be inferred, is due mainly to moths bred from the previous larval populations in winter crops.

4. *December.*

The graphs misrepresent the levels of incidence at this time, as oviposition on natural food-plants is excepted because of inability to express egg numbers in comparable terms of eggs per the area under survey.

It is known from records on sampled areas of weeds and from the weight and course of egg-laying on sample units in cultivated crops that a peak of laying occurs in December. The acreage of cultivated crops at this time of year, from which the data in fig. 2 are drawn, is too small, relatively, to give expression to the order of laying.

5. *January to April, inclusive.*

Rain-grown crops, particularly cotton and maize, occupy the scene. Oviposition in quantity ensues only upon the coming into flower of the early-planted crops, particularly maize. The constancy of the interval between planting and flowering of maize and cotton allows it to be known when the infestation will commence. In fig. 2 this is shown to have held for one unusually early, one unusually late, and three of the more usual planting occasions. The major bollworm attack falls in January and February. Subsequent activity is on a diminished scale, and there is discordance between the expected and actual waves of bollworm bred from the January–February larval populations, for reasons of which discussion is deferred.

Mention has been made of the possibilities of moths entering the environs of Barberton from outside sources of breeding. The subject may be considered here as it bears on the recurring aspect of the information presented above.

It was determined in two years' observations that the quiescent period, May–July, applies to a lesser degree in a lower, warmer district devoted to orchard and vegetable farming some thirty to forty miles distant from the Cotton Experiment Station. Extensive moth emergence occurs there from April onwards, resulting in waves of oviposition that are out of rhythm with the local emergence and oviposition. It is to be expected that moths migrating thence to Barberton would signalise their presence in quantity, particularly in June and July, by oviposition on early winter crops, but also at other times in conflict with the known train of local events. On no occasion has there been a suggestion of moth immigration. The question of inter-district movement of moths has also received attention. Selecting an extreme case of two adjacent farms under record in Natal, one purely dry-farming, the other combined irrigation and dry-farming (but with emphasis on winter-crop production), it was found for three successive seasons that the weight of oviposition in the dry-farming instance was of a relatively low order, entirely accountable for by the extent of pre-breeding on natural food-plants. Similar evidence emerges from studies in European and native-grown crops in Swaziland.

Moth Flights and the Origin of Moths.

As a routine procedure larval populations have been assessed at all points of record and representative samples have been drawn weekly for various insectary and laboratory purposes. The adult larvae in the weekly samples have been removed to individual cages in the open, provided with food of the nature partaken in the crop wherein collected, and allowed to pupate naturally. Moth emergence in the cages is recorded and in the aggregate is viewed to supply information on the course of moth incidence. Variations in the field population of mature larvae are reflected in the samples drawn and, with reservations, an indication of moth flights in nature is to be expected from evidence obtained in miniature from the caged material. Whenever concentrated for observation, unprotected larvae and pupae are destroyed to a much greater extent than applies under ordinary field conditions. To avoid the loss of material, pupation cages have been set out as illustrated in Plate I. Each unit comprises 49 individual cages contained in a metal frame set nine inches deep in the soil. The bottom is pierced for drainage and the holes covered with fine mesh wire. Surrounding the perimeter of the frame is a trough containing a solution of kerol and water. These measures and a surround of netting to exclude blown vegetable matter have minimized losses through predators. It should be stated that the soil moisture content, determined twice-weekly, at pupation depth within the frames agrees very closely with the mean moisture content in summer crop lands and lands unirrigated in the off-season. With regard to winter-irrigated crops, it has been determined that pupation occurs normally in the semi-dry top of the ridged soil containing the line of plants; the moisture content at pupation depth is higher here for brief periods than it is in the frames, but no significant difference has been

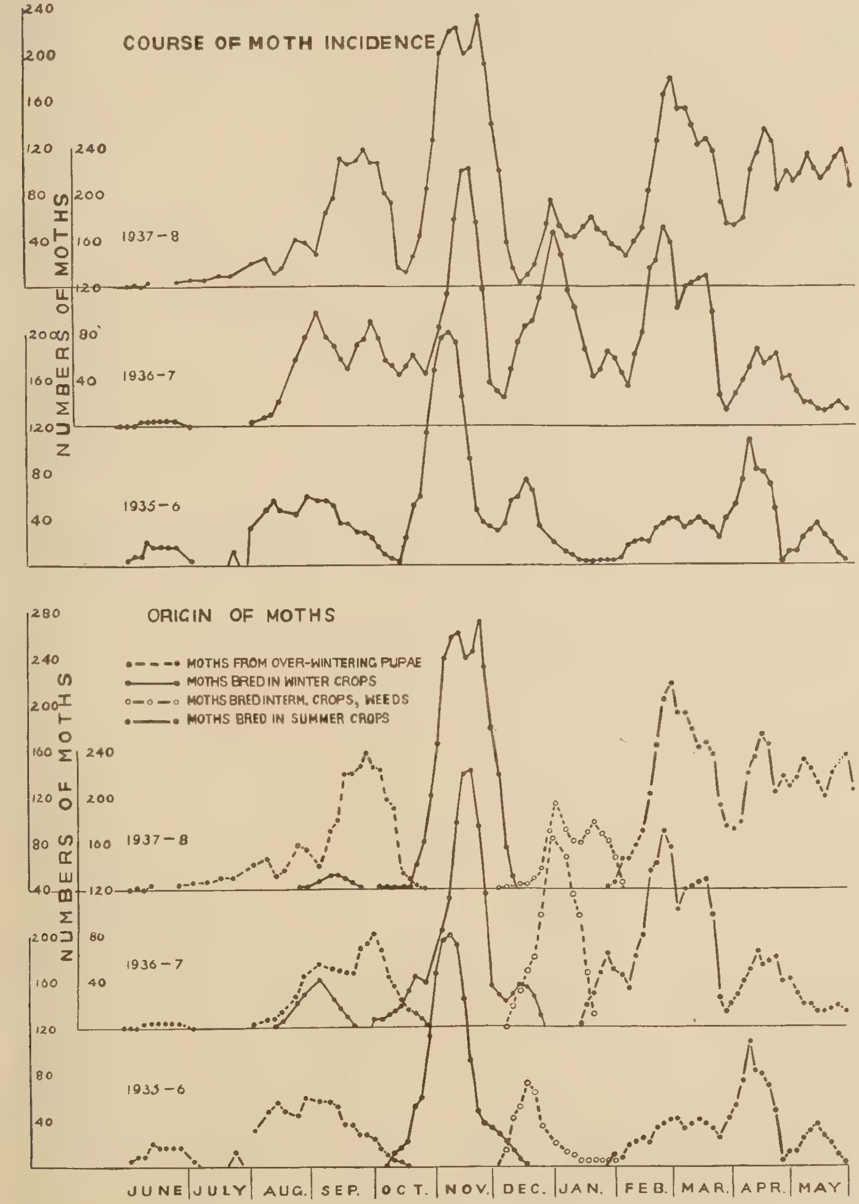

Fig. 5. Moth incidence and origin of moths.

found experimentally between the duration of the pupal phase in the frames and in positions in the soil ridges. Pupae formed in the winter months do not enter a diapause. Amongst those pupae formed and in diapause at the close of the summer season earlier break-up of dormancy appears to be induced by higher soil moisture, and some discrepancy between records in the frames and the field no doubt results from the difference in moisture conditions. Temperatures in all cases, particularly minimum temperatures, agree fairly closely. Plate II illustrates single cages set out alongside rows of plants in simulation of field conditions ; the cages have enlarged holes in the wire for the passage of predators, but the escape of moths and pupal parasites is prevented. Series of cages in this category are utilized in a randomized manner which aims at reproducing alongside plants the scatter of pupation sites that occurs in the field from a moderately heavy infestation over the period larvae are present ; similar lay-outs are used in various types of crop. The measure allows for the presence of the insect community associated with a crop, including the predators pertinent to the case.

Apart from the aggregate picture of moth incidence obtainable as above, the origin of individual moths is a matter of record, and the whole may be divided readily into parts according to origin, which may embrace any sphere of breeding in the "Bollworm Year."

Data for three years from moth emergence in the protected cages are given graphically in fig. 5 : the upper three graphs depict the sum of moth incidence, and in the lower three the same data are shown subdivided according to the source of moths. For correct presentation and with the object of establishing the complicity of moths in relation to the periods of oviposition witnessed, the graphs are drawn from cumulative figures based on the mean oviposition life of moths applicable to the time of year, as given in Table II from insectary records.

It has been determined that egg-laying by individual moths follows a most irregular course, and as often as not, high numbers are laid at both the commencement and the close of the oviposition history ; when calculating the means, moths are retained therefore for the whole of the oviposition life periods.

As moths emerging from diapausing pupae (which here are termed over-wintering pupae) occasion the resumption of activity following the quiescent period (page 331), it was expedient first to ascertain the limits of their participation ; similarly for

TABLE II.

Oviposition Life of H. armigera ; *Mean of Monthly Records.*

Month	Number of records. Fertilized ♀♀	Mean number of days oviposited	σ	C.V. per cent.
June	24	23·08	4·85	21·01
July	34	20·00	5·85	29·25
August	29	16·86	4·98	29·54
September	29	16·31	5·75	35·25
October	24	16·00	3·85	24·10
November	31	13·09	3·40	25·96
December	21	10·14	2·29	22·58
January	27	12·29	3·38	27·50
February	29	12·00	3·40	23·00
March	30	12·11	3·75	30·92
April	22	13·10	3·20	26·90
May	18	23·30	4·82	20·69

Moths were fed with a solution of glucose and fructose based on the constitution of nectar produced at the extra floral glands of cotton, a natural food of *H. armigera* (Parsons[9]). In computing the participation of moths, allowance has been made, where numbers were considerable, for short-lived moths bred from certain food-plants.

moths bred in the winter crop period and in the period intermediate between winter crops proper and rain-grown crops. Knowledge of when moths in these categories ceased participation was required to establish the sources whence moths initiating the infestation in summer crops are derived. In fig. 5 are shown the limits of participation of moths from (1) over-wintering pupae, (2) winter-bred moths, and (3) moths bred in crops and natural food-plant areas in the intermediate period. A chief point of interest in this information is the remarkably close agreement in the three years of the dates at which the last representative attributable to the three sources ceases activity,[*] viz. :—

	1935–36	1936–37	1937–38
1. Moths from over-wintering pupae	18th Oct.	29th Oct.	25th Oct.
2. Moths bred in winter crops	17th Dec.	24th Dec.	10th Dec.
3. Moths bred in crops and weeds in the period between winter and summer crops	30th Jan.[†]	20th Jan.	3rd Feb.

Recalling that the food-plant situations have been canvassed thoroughly and sampled continuously for records and material, the recurring agreement of these cessation dates is acceptable as a working basis. The recurrence of periods II and III in the oviposition records of fig. 2 is explicable in the light of the analysed moth incidence. Considering now the category of moths initiating the first attacks on summer crops, it is clear from the evidence in figs. 5 and 2 that only moths from No. 3 source can have participated ; this is so even for the year of earliest planting, 20th October, 1936. The two factors, constancy of the interval between planting to appearance of flowers and the oviposition-flowering relationship, indicate very closely when the first bollworm attack on summer crops, including cotton, will occur. The point under moth flight No. 3 at which the crops will become susceptible to oviposition may also be calculated to some extent from the planting dates ; clearly, in an early planting season the crops are exposed to a longer first attack. In a very early planting season, *i.e.* September planting, as attempted occasionally by cotton-growers, crops are susceptible also to oviposition by moths bred in the winter crops and there is a prospect of exceptionally heavy bollworm attack. Although further information is sought in confirmation of the time relationships referred to, they form the present basis of measures for the reduction of bollworm in the cotton crop, whether by diverting moths to counter-attractive crops planted conformably, or by the use of insecticides. In our experience diversion is the most effective method (*cf.* fig. 4) and it is attained without detriment or additional expense by simple alterations in the planting programmes. Insecticides are regarded as an expensive accessory, for employment only in years when egg counts on cotton give warning of heavy attacks to follow.

Allowing for the influence of rains and gales the successive flights of summer-bred moths shown in fig. 5 agree fairly well with the periods of oviposition given in fig. 2. There is, however, a wide difference in the relative moth and egg populations. Differences in this respect are due mainly to a high mortality of adult larvae in the field when seeking to pupate and to subsequent destruction by predators and other causes of larvae that have pupated—losses not suffered in the protected cages. Data from the unprotected cages are giving some information as to the nature and causes of losses due to natural enemies, but the investigation has not been in progress long enough for discussion here.

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[*] In the Reports from Experiment Stations, E.C.G.C. for 1937–38, dates were given differing from the above by a week to ten days. But in the previous instance the dates were based on cumulative figures at weekly intervals, whereas on the present occasion daily data have been used and some corrections have been made for abnormal cases of oviposition.

[†] Planting rains did not occur until late December. The prolonged hot, dry period restricted growth of natural food-plants and breeding of bollworm was on a most reduced scale. Moths in No. 3 category also lay to a slight extent on weeds in growth with flowering summer crops.

Summary.

Methods for the quantitative survey of the incidence of *Heliothis armigera* have been in continuous operation in the Barberton area of the Eastern Transvaal from 1929 to the present ; since 1933 the Survey was operated similarly in Swaziland and Northern Natal.

It was accepted early that the bollworm situation in cotton, which primarily it was desired to ameliorate, depends largely upon the influences exerted by other food-crops of the insect grown prior to and in association with cotton, and the investigations were instituted with a view to acquiring the fullest information on the incidence, habits and reactions of *H. armigera* with respect to the chain of cultivated and natural food-plant situations existing under differing climatic conditions in the course of the year.

The present paper is the first of a series communicating the results of investigations which proceed in various directions from information supplied by the Cotton Pest Survey centred upon Barberton. The paper deals with the annual course of bollworm incidence as indicated, in the first instance, by egg counts taken twice-weekly, year by year, in examples of all food-plant situations according to methods of sampling and calculation devised here.

Data are given for five years' observation in concrete examples of situations in the environs of the Cotton Experiment Station, Barberton, the Cotton Station serving to represent the summer crop phase ; the circumstances reported from these examples accord in all essential features with those applicable to the much wider areas under record. Information revolving on successive calculations of eggs-per-crop-area is utilized for discussion and graphic depiction of the course of bollworm activity annually, and evidence is supplied of periodical incidence of a markedly recurring nature. A " Bollworm Year " is defined and this may be divided for reasons given and reviewed (pp. 331, 332) into five periods of varying activity, which are related to the habits of the insect, particularly diapause phenomena, climate and food. Circumstantial evidence is provided that immigrant moths have not been a contributing factor.

The close association of oviposition with the period of flower production on the food-plants of *H. armigera* is emphasised. This association in conjunction with constancy in the interval, seeding-to-appearance-of-first-flowers, of cotton and maize, the predominant rain-grown crops, postulates when egg-laying on these crops may be expected to commence in quantity ; data given for five years of widely differing planting dates evince the accuracy of forecasts so based.

The heaviest bollworm attack of the cotton-growing season has fallen always within a month to six weeks from the commencement of flowering in maize and cotton. It is particularly important to minimize losses amongst the cotton fruit set within this period, as it contributes a high proportion of the crop yield, and measures for evasion and reduction of bollworm in cotton have been focussed accordingly. A preference of the moth to oviposit on maize has for long been utilized in diversion of moths from cotton at critical times and the success of the measures is indicated in a figure displaying for five years the relative oviposition on crops of cotton and maize of variable acreage.

Evidence obtained from studies of moth emergence serve to explain the yearly recurrence of the periodical oviposition witnessed. There is a remarkable similarity in the times of year at which moths from successive sources cease activity. The information supplies a clear indication of the origin of moths which occasion the initial infestation of cotton and other summer crops and aids substantially in anticipating the arrival and duration of the first summer attack according to planting dates.

Acknowledgments.

The author's colleagues, Mr. H. Hutchinson and Mr. P. A. Bowmaker, and their staffs, stationed in Swaziland and Natal respectively, have co-operated most extensively in the field investigations on cotton insect pests. The results of their work, which receive little specific reference in the present instance, have supplied much confirmatory data from unusually wide areas of record.

It is desired to record appreciation for the unfailing and exceptional assistance rendered by Mr. C. E. Booth in his capacity as supervisor of the native enumerators at Barberton.

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APPENDIX I.

Natural Food-plants of *Heliothis armigera*.

No.	Name	Family	Remarks
1	*Acalypha segetalis*, Müll Arg.***	Euphorbiaceae	Abundant in cultivated lands (Northern Natal).
2	*Amaranthus hybridus*, L. s.l.*	Amarantaceae	Abundant only vicinity cattle kraals, flowers sparsely in dry season.
3	*Amaranthus thunbergii*, Moq.***	”	Common land weed, mostly dries off May and June; occasional green patches persist and flower sparsely through winter, abundant after rains.
4	*Bidens pilosa*, L.*	Compositae	Always abundant, very reduced but persistent flowering in dry season.
5	*Chenopodium hircinum*, Schrad.*	Chenopodiaceae	Relatively uncommon.
6	*Chenopodium murale*, L.**	”	Abundantly in flower on irrigated lands in September–December.
7	*Cleome monophylla*, L.**	Capparidaceae	Of importance in bollworm maintenance (Swaziland) August onwards.
8	*Datura ferox*, L.*	Solanaceae	Contributes as occasional food-plant in November and December.
9	*Datura stramonium*, L.***	”	Abundant November–January period; slight quantities in flower during dry season.
10	*Hoslundia opposita*, Vahl., var. *decumbens*, Bak.**	Labiatae	Of importance in bollworm maintenance (Swaziland) from August until rain-grown crops appear.
11	*Leucas martinicensis*, Ait.**	”	Reported as food-plant (Northern Natal) prior to rains.
12	*Malvastrum tricuspidatum*, A. Gray***	Malvaceae	Contributes as food-plant mainly in the November–January period
13	*Nicandra physaloides*, Gaertn.***	Solanaceae	As for No. 12, also maintains bollworm in dry season, particularly in Lower Swaziland and Northern Natal.
14	*Ocimum americanum*, L.**	Labiatae	Of importance with 7, 10 and 13 prior to rains in Swaziland.
15	*Orthosiphon serratum*, Schlech.**	”	As for No. 14.
16	*Physalis angulata*, L.**	Solanaceae	Frequently associated with *H. armigera* but eggs generally confused with those of *H. assulta*. Abundant November–January.
17	*Sida rhombifolia*, L., var. *riparia*, Burtt Davy**	Malvaceae	Abundant November–January; only slight quantities in flower during dry season, except along streams.
18	*Sida* sp.**	”	Confused in records with No. 17.
19	*Solanum nigrum*, L.*	Solanaceae	Few records.
20	*Sonchus oleraceus*, L.***	Compositae	Moderately abundant mainly in November–January.
21	*Sonchus asper*, L.**	”	As for No. 20.
22	*Tagetes minuta*, L.*	”	Abundant, but flowers sparsely dry season; eggs and larvae very infrequently found.
23	*Xanthium pungens*, Willd.***	”	Occasional green patches persist and flower sparsely in the dry season, abundant after rains.

Cassia siamea (Leguminosae), introduced from Northern Rhodesia for windbreak purposes, serves occasionally when in flower but apart from doubtful records on *Crotalaria* spp., no instances have been recorded of eggs and larvae on the very many indigenous species of Leguminous trees.

* Rarely associated. ** Frequently associated. *** Most frequently associated.

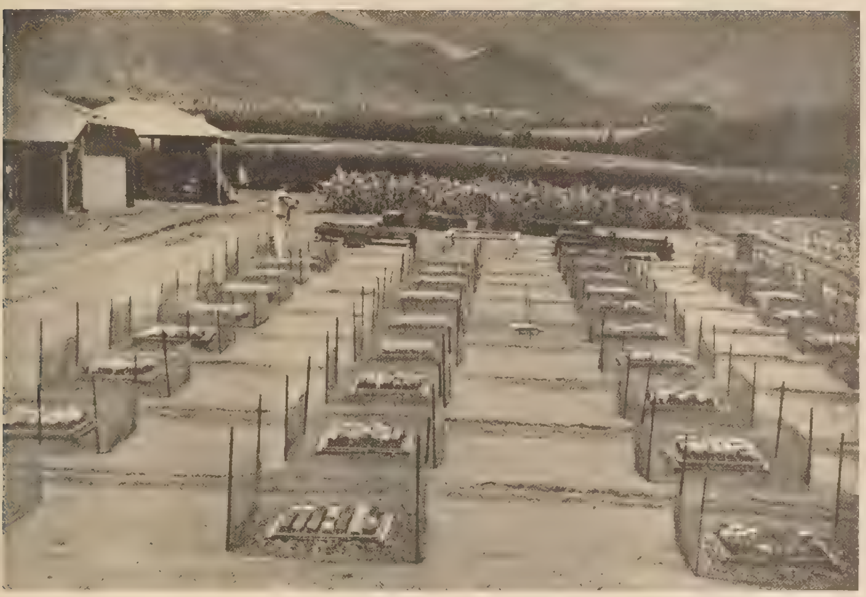
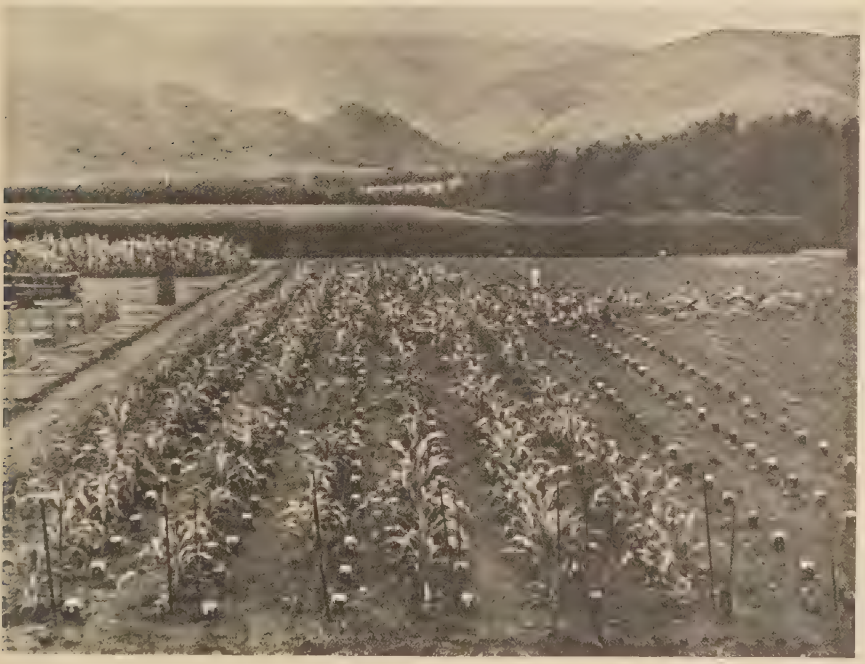


Fig 1. Individual pupation cages in protected sites.



John Bale Sons & Curnow L^td London.

Fig 2. Individual pupation cages in unprotected sites.

ON THE GENERA OF THE DIPRIONIDAE (*HYMENOPTERA SYMPHYTA*).

By Robert B. Benson, M.A.

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In preparing the part dealing with the Diprionidae in a synopsis of the British sawflies I came upon several morphological characters that, if used or made more use of, would greatly facilitate the naming and classification of this economically

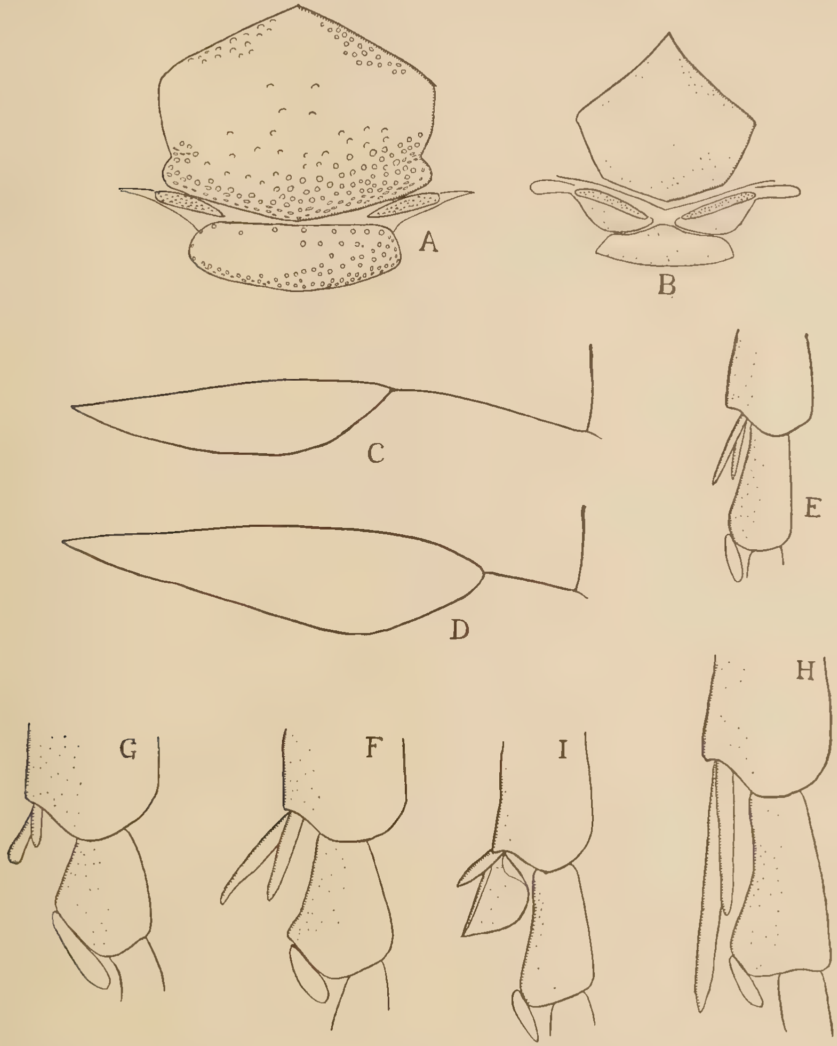

Fig. 1. A–B : Meso- and meta-scutellum with cenchri in A, *Diprion pini* (L) ; B, *Neodiprion sertifer* (Geoffroy).
C–D : Anal cell of hind-wing with pedicel in C, *Diprion pini* (L) ; D, *Neodiprion sertifer* (Geoffroy).
E–I : Apex of hind tibia with spurs and basitarsus with pulvillar pad in female of E, *Microdiprion pallipes* (Fallén) ; F, *Neodiprion sertifer* (Geoffroy) ; G, *Zadiprion* sp. ; H, *Nesodiprion japonicus* (Marlatt) ; I, *Gilpinia polytoma* (Hartig).

important group of insects. A comparison between *Neodiprion* and *Diprion* (s.l.) revealed at once striking differences in the shape of the meso-scutellum, the sculpture of the abdomen and the anal cell in the hindwing, characters easily visible in the field and therefore of great importance to the economic entomologist. *Diprion pini*, L., and *similis*, Hartig, were found to differ from the other *Diprion* species, among other things, in their small cenchri, a character easily visible in the field, and the genus has been divided.

Turning next to representatives of the family in other parts of the world, as many specimens as possible were got together in an attempt to draw up simple generic keys. In so doing I have made use of Rohwer's generic revision (1918) and Ross's revision of the nearctic genera (1937).

The central European sawflies of this family can be identified in the adults with the help of Enslin (1917) and in the larvae with Enslin (1914).

I am much indebted to the following :—

Drs. L. Berland (Paris) and W. Horn (Berlin) for the loan of the types of *Lophyrus gaullei*, Konow, to Dr. H. Ross (Urbana) for specimens of *Zadiprion townsendi* (Cockerell), and to Miss Grace Sandhouse (Washington) for checking what I have said about *Neodiprion* and *Augomonoctenus* with the material in the Museum at Washington, for giving me information about *Diprion nipponicus*, Rohwer, and for sending me specimens of *Nesodiprion japonicus*, Rohwer.

Key to World Genera of Diprionidae.

1. Scutellum blunt in front, forming an angle of much more than 90° (fig. 1, A) ...2

—. Scutellum acute in front, forming an angle of 90° or less (fig. 1, B)...............6

2. (1) Abdomen polished, without transverse rugulous sculpture ; anal cell of hind-wing with a short pedicel (fig. 1, D), not longer than the greatest breadth of the cell ; inner hind apical tibial spur quite as long as basitarsus (fig. 1, H) ; malar space about as long as 2nd antennal segment or less. [Antenna biramose in both sexes, though the rami are shorter in the ♀ ; 1st cubital cell of forewing (as indicated by stub of 1st cross-vein) not more than ½ as long as broad ; anal cell narrowed at about ⅓ its length from the base and with a short cross-vein at about ⅗ from the base ; cenchri very large so that the distance between them is not more than ½ the breadth of one ; hind tibia slightly curved ; ♀ pulvillus of hind basitarsus about ½ as long as the apical breadth of the basitarsus ; claws with a small basal tooth. Japan and China. Type : *Lophyrus japonica*, Marlatt ; contains also *biremis*, Konow (China)]...........
Nesodiprion, Rohwer 1910

—. Abdomen dull, with transverse rugulous sculpture ; anal cell of hind-wing with a long pedicel (fig. 1, C) much longer than the greatest breadth of the cell ; inner hind apical tibial spur much shorter than basitarsus (fig. 1, E) ; malar space at least longer than the 2nd antennal segment 3

3. (2) Cenchri small, being at least 1½ times further apart than the breadth of one (fig. 1, A) ; metascutellum large, being at least as long as the breadth of a single cenchrus 4

—. Cenchri large, being generally close together or at least scarcely further apart than the breadth of one (*cf.* fig. 1, B) ; metascutellum shorter than the breadth of a single cenchrus...5

4. (3) Antenna of ♀ distinctly tapering, not serrate above ; the 3rd segment longer than the 4th ; the 4th with a projection. Antenna of ♂ not more than 26 segmented and biramose except for the last 2 or 3 segments. [Malar space as long as the basal breadth of the mandible and several times longer than the 2nd antennal segment ; forewing with 1st cubital cell (as indicated by stub of 1st cross-vein) not more than ½ as long as broad ; anal cell narrowed at a point just under ⅓ from the base and with a short cross-vein just behind the middle ; anal cell of hindwing has a long pedicel, much longer than the greatest breadth of the cell ; ♀ pulvillus of hind basitarsus about ½ as long as the apical breadth of the basitarsus ; claws with a small sub-basal tooth. Palaearctic, introduced into North America. Type : *Tenthredo pini*, L. Three species : *pini*, L., *similis*, Hartig, and *nipponicus*, Rohwer]....................*Diprion*, Schrank 1802.

—. Antenna of ♀ not tapering, serrate above and below ; segments 3 and 4 subequal, ring-like and without projections. Antenna of ♂ 30–32 segmented ; apical 6 segments with only one ramus. [Otherwise as in *Diprion*, Schrank. Palaearctic. Type : *Lophyrus* (*Macrodiprion*) *nemoralis*, Enslin. Monotypic] .... *Macrodiprion*, Enslin 1917.

5. (3) Malar space 2 or 3 times as long as 2nd antennal segment ; ♀ antenna serrate below or with rami much shorter than the breadth of the segments bearing them ; in the forewing the width of the anal cell at the basal contraction is greater, usually much greater, than the width of the anal vein at that point and the anal vein (except in *D. virens*, Klug) is not angled at the contraction ; inner apical tibial spur in ♀♀ of some species expanded into a leaf-like structure (fig. 1, I). [Antenna serrate below in ♀, bipectinate in ♂ ; forewing with 1st cubital cell (as indicated by stub of 1st cross-vein) not more than ½ as long as broad ; anal cell narrowed at a point just under ⅓ from base and with a short cross-vein just behind the middle ; anal cell of hindwing has a long pedicel, much longer than the greatest breadth of the cell ; ♀ pulvillus of hind basitarsus about ½ as long as the apical breadth of the basitarsus ; claws with a small sub-basal tooth. Palaearctic, Oriental and introduced into North America. Divided into 2 groups as follows : (a) The *polytoma* group : ♀ with inner hind tibial spur expanded into a leaf-like structure (fig. 1, I) ; includes *fennica*, Forsius, *pallida*, Klug, *polytoma*, Hartig, and *virens*, Klug (Europe and Siberia). (aa) The *socia* group : ♀ with inner tibial spur normal (fig. 1, E) ; includes *abieticola*, Dalla Torre, *frutetorum*, F., *laricis*, Klug, *rufiventris*, Zirngiebl, and *socia*, Klug (Europe and Siberia) ; ? *hakonensis*, Matsumura ; ? *koreana*, Takagi (Korea) ; *marshalli*, Forsius (China), and ? *indica*, Cameron (India). Of the species queried, *indica* is represented in the British Museum by the single ♂ type, while *hakonensis* and *koreana* have not been seen and are also not possible to place with certainty from the original descriptions. Type : *Lophyrus polytomus*, Hartig.]...........*Gilpinia*, gen. nov.

—. Malar space scarcely longer than the 2nd antennal segment ; ♀ antenna below with rami on the flagellar segments, each ramus being longer than the breadth of the segment bearing it except at the extreme apex of the antenna ; in the forewing the anal cell is very strongly contracted basally so that the width of the cell at the contraction is scarcely greater than the width of the anal vein at this point ; the anal vein strongly angled at this point ; hind apical tibial spurs normal. [Otherwise as in *Gilpinia*, gen. nov. ; ♂ unknown ; Algeria. Type : *Lophyrus gaullei*, Konow. Monotypic]..............*Prionomeion*, gen. nov.

6. (1) Anal cell of forewing divided into two by a medial constriction ; 1st cubital cell (as indicated by stub of 1st transverse cubital vein) about as long as its apical breadth ; transverse median vein strongly oblique ; anal cell of hindwing with a stalk longer than the breadth of the cell (fig. 1, C) ; ♂ antenna uniramose with flagellum strongly curved apically..7

—. Anal cell of forewing only slightly contracted sub-basally, not divided, and with a cross-vein behind the middle ; 1st cubital cell is much shorter than the apical breadth, transverse median vein suberect ; anal cell of hind-wing with a stalk shorter than the breadth of the cell (fig. 1, D) ; ♂ antenna with at least 10 basal segments, biramose, with flagellum not strongly curved apically..................8

7. (6) Supra-clypeal area of head below antennal sockets, raised above level of clypeus ; intercostal vein in forewing present ; head and thorax not metallic. [Pulvillar pad of hind basitarsus shorter than the apical breadth of the basitarsus ; claws with a small sub-basal tooth ; each of the cenchri scarcely as broad as the distance between them. Holarctic. Type : *Tenthredo juniperi* L. ; 6 species] ....*Monoctenus*, Dahlbom 1835.

—. Supra-clypeal area of head not tuberculate, confluent with profile of clypeus ; intercostal vein absent ; head and thorax metallic. [Otherwise as in *Monoctenus*, Dahlbom. Nearctic. Type : *Augomonoctenus libocedrii*, Rohwer ; monotypic] .... *Augomonoctenus*, Rohwer 1918.

8. (6) Abdomen with the middle segments shining and polished above, without any surface sculpture (the sculpture may be developed slightly in *Microdiprion* but then the tarsal claws are simple without sub-basal tooth) ; ♀ with pulvillar pad on hind basitarsus shorter than the apical breadth of the basitarsus, hind apical tibial spurs normal in form, with the inner one at least longer than ½ the apical breadth of the tibia (figs. 1, E, F) ; ♂ antenna with all but last segment of flagellum biramose ; cenchri usually as close as or closer together than ½ the breadth of one...9

—. Abdomen with the middle segments dull above with dense coriaceous or transversely rugulose surface sculpture (in the ♀ of *Z. rohweri*, Middleton, this sculpture is sub-obsolete) ; tarsal claws always with a sub-basal tooth ; ♀ with pulvillar pad on hind basitarsus longer than apical breadth of basitarsus, and the hind apical tibial spurs subclavate and not longer than ½ the apical breadth of the tibia (fig. 1, G) ; ♂ antenna with 5 apical segments of flagellum uniramose ; cenchri at least as far apart as ½ the breadth of one and generally almost as far apart as the full breadth of a cenchrus. Nearctic. [Type : *Diprion grandis*, Rohwer ; 4 species ; keyed by Middleton 1931] .... *Zadiprion*, Rohwer 1918.

9. (8) Claws with a small sub-apical tooth ; ♀ hind basitarsus expanded towards the apex so that it is less than twice as long as broad (fig. 1, F). [Abdomen with 1st tergum usually almost impunctate ; middle terga entirely without coriaceous or rugulose sculpture. Nearctic with one species, *N. sertifer*, Geoffroy, in Europe. Type : *Lophyrus lecontei*, Fitch. Many nearctic species now in need of revision] ....*Neodiprion*, Rohwer 1918.

—. Claws simple without sub-apical tooth ; ♀ hind basitarsus normal, as in ♂, and more than twice as long as broad (fig. 1, E). [Abdomen with 1st tergum dull, with rough surface ; coriaceous sculpture sometimes partially developed on middle terga. Europe. Type : *Lophyrus pallipes*, Fallén ; 2 species]......... *Microdiprion*, Enslin 1917.

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A NEW MALAYAN SPECIES OF *HELOPELTIS* (RHYNCHOTA, CAPSIDAE).

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Entomologist, Department of Agriculture, S.S. & F.M.S.

The new species described herein was found, in the first instance, on cacao (*Theobroma cacao*, L.) at the Central Experiment Station, Serdang, Selangor, Federated Malay States. Later on, a few specimens were caught on the leaves of annatto (*Bixa orellana*, L.) plants situated at about two hundred yards from the area planted with cacao.

Up to the present no records have been received of damage to tea by this species, although moderately large areas planted with tea are present in the near vicinity. In the laboratory, however, young tea shoots were readily accepted.

Helopeltis theobromae, sp. n.

Colour.—♂. Antennae: segment 1 testaceous, apically piceous, basally green; tubercles piceous; remaining segments piceous. Head green; vertex and clypeus

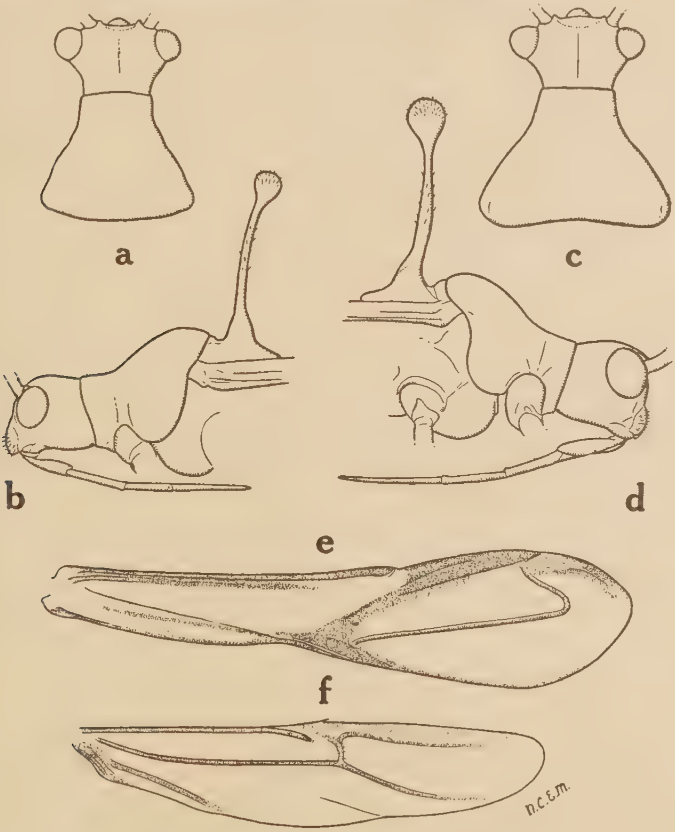

Fig. 1. *Helopeltis theobromae*, sp. n.
a. Head and pronotum from above, male.
b. ,, ,, ,, ,, side, ,,
c. ,, ,, ,, ,, above, female.
d. ,, ,, ,, ,, side, ,,
e. Hemielytron. **f.** Wing.

suffused with piceous ; eyes piceous ; rostrum testaceous. Thorax piceous with an ochreous spot on posterior lobe laterally ; scutellum testaceous, suffused with piceous basally, apex piceous ; pro- and mesosterna piceous ; metasternum green. Meso- and metapleurae green. Abdomen green. Legs : femora testaceous with suffused piceous spots ; tibiae testaceous, basally piceous and with some interrupted piceous annulations in basal half. *Hemielytra* hyaline, faintly infumate and iridescent ; cuneus and venation pale testaceous, infumate.

Colour.—♀. Similar to that of ♂ with the following exceptions : pronotum with collar dorsally and laterally pale flavous, ventrally blackish green ; remainder of anterior lobe, acetabula and posterior lobe narrowly anteriorly, blackish green, medially ochreous, basally broadly and laterally narrowly piceous. Scutellar spine testaceous, broadly black apically and with a sub-basal black annulation. Abdomen green, dorsally and ventrally in apical half blackish green.

Structure.—♂. Antennae : basal segment moderately thick, minutely tuberculate and setose, thicker apically, longer than head, pronotum and scutellum together ; segment 2 slender, minutely tuberculate and setose, nearly twice as long as segment 1 ; segment 3 a little shorter than 2, with abundant short setae ; segment 4 a little more than one-third as long as 3, with abundant short setae. Head a little wider than long, measured between the eyes, less than half as long as pronotum ; tylus with minute setigerous tubercles ; eyes prominent, ovate ; internal margins of antennal tubercles moderately prominent ; basal segment of rostrum extending to middle of postocular. Scutellum with apical spine erect, feebly curved, longer than pronotum. Hemielytra extending beyond apex of abdomen by about one-third of their length. Legs : femora somewhat nodulose and sparsely tuberculate ; tibiae with abundant low setigerous tubercles ; apical segment of tarsi a little longer than remaining two segments together.

In recently killed specimens the apex of the scutellar spine is spherical, but within a few hours the membranous apical portion collapses with the result that the spine appears truncate apically.

Measurements.	♂	♀
Total length	4·80 mm.	5·70 mm.
Hemielytra	4·80 mm.	5·50 mm.
Greatest pronotal width	1·30 mm.	1·50 mm.

Described from a series of males and females.

FEDERATED MALAY STATES : Selangor, Serdang, viii–xii.1938 (*N. C. E. Miller*).

Type (male) and a series of paratypes in the British Museum (Natural History).

OBSERVATIONS ON *GLOSSINA FUSCIPLEURIS* AND OTHER TSETSES IN THE OYANI VALLEY, KENYA COLONY.

W.

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(Plates XI and XII.)

The Oyani Valley is in the South Kavirondo native reserve of Kenya Colony. The river from which the valley takes its name rises in the Kilgorris groups of hills in and near the south-west corner of the Masai Reserve. The Oyani enters South Kavirondo at a point about 1°0′ South by 30°35′ East ; it flows in a general north-westerly direction through the Kanyamkago location and joins the Kuja River about eighteen miles above the junction of the Kuja and the Gori Rivers.

Four species of tsetse-flies find favourable haunts in the valley. They are *Glossina pallidipes*, *G. fuscipleuris*, *G. brevipalpis* and *G. palpalis*. Their distribution along the Oyani River and its tributaries is not regular and continuous ; it differs with the character of the vegetation. Breeding-places of all four species are largely confined to narrow belts of bush ; but the range of dispersal covers most of the Oyani catchment area ; and, in places, even extends over the Gori-Oyani watershed.

The location, or sub-tribal area, of Kanyamkago is seriously affected by the tsetse-infestation, which appears to be spreading. The local native inhabitants who have hitherto remained in the area are eager to protect the existing fly-free localities where the cattle are concentrated, and to adopt some measures for reclaiming those localities from which the tsetses have driven them.

The natives of the location are by no means indolent ; nor have they yet acquired that apathy that tends to develop among natives where tsetse-flies have long made their lives fortuitous. On the contrary, they cultivate the occupied land intensively and produce a variety of food and cash crops. They possess many herds of cattle, which are now restricted to the north-western corner, in an area of about thirty-eight square miles, or approximately one-quarter of the whole location. With the advance of the tsetses and the consequent losses from animal trypanosomiasis, the people have abandoned most of Kanyamkago ; they will not stay in any locality where it is not possible to pasture the majority of their stock with reasonable safety. It is true that there are isolated families still clinging to their old homes in the fly-belt. Their cattle are usually in charge of a friend or relation residing in fly-free native areas or possibly on a European farm many miles away. Most of the old inhabitants have left the area and have either succeeded in finding new homes and land in other neighbouring locations or have moved *en bloc* to Tanganyika, thus reducing the population of Kanyamkago, where their energy might be directed to the amelioration of conditions or at least to checking the advance of the tsetses.

The present inhabitants offer a natural, simple and logical argument for their dislike and fear of the fly-infested areas ; for their inability to prevent the spread of tsetse and their surrender of the country to the fly. Their desire for meat and milk, as well as food crops to maintain good health, their ability to purchase stock with cash acquired for crops, prompted the natives to appeal to the Administrative authorities for assistance to protect the north-west corner of the location from further advances by the tsetses and to reclaim some of the infested areas. They were not able, on their own, to attack the flies of whose habits they were ignorant. They had been encouraged by the results of experiments conducted to control tsetse-flies in the Kuja River and Lambwe Valley areas of South Kavirondo.*

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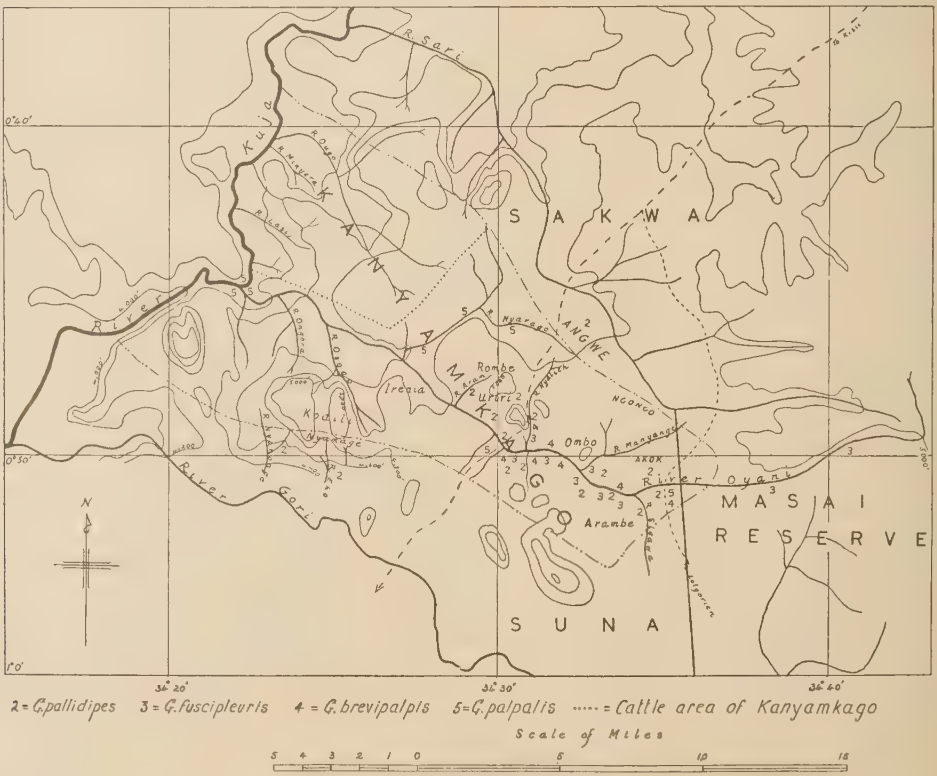
*These experiments are financed by a grant from the Colonial Development Fund.—E.A.L.

The lack, or irregularity, of a balanced diet may be responsible for the "indolence" or "lethargy" encountered so often in natives in fly areas. In Kanyamkago, as in other parts of Kavirondo, they state that they dread human trypanosomiasis less than they do animal trypanosomiasis. They can avoid the former by keeping away from the infested, heavily forested rivers, but they cannot evade the latter so easily; and, in any case, the losses from animal trypanosomiasis deprive the people who have escaped from the human disease of one of the chief requirements for maintaining good health.

The author was requested by the Administration to examine the situation in the Oyani Valley and to investigate the possibility of preventing further encroachment by the tsetses and to suggest schemes for reclamation.

It will be appreciated, in view of the present knowledge of the reaction of the several species to attempts at control, that the practical aspect of the problem in the Oyani Valley is not a simple one; and though suggestions based on a general policy of protection, gradual reclamation and progressive development have been submitted, they will not be considered at length in this communication.

Apart from the more practical aspect, the observations made in the Oyani are of interest in that they reveal the existence of four species of *Glossina* in a relatively narrow strip of country; they connect and continue the problems of distribution of fly-belts in the Masai and the South Kavirondo reserves; and they disclose the breeding-places and puparia of *G. fuscipleuris*. They show also that there is a high degree of parasitism of puparia which is due to *Trichopria capensis*, Kieff. var. *robustior*, Silv.—a parasite recovered from wild puparia and subsequently reared in the laboratory.



0°40'
0°50'
1°0'
34°20'
34°30'
34°40'
R. Sari
Kuja
KANYAMKAGO
SAKWA
NYANGWE
NGONGO
Rombe
Ireala
Ombo
River Oyani
MASAI RESERVE
SUNA
Arambe
River Gori
River
N
2 = G. pallidipes 3 = G. fuscipleuris 4 = G. brevipalpis 5 = G. palpalis ..... = Cattle area of Kanyamkago
Scale of Miles
5 4 3 2 1 0 5 10 15

Fig. 1. Map.

Vegetation.

Generally, it may be said that the Oyani has a narrow band of riverine forest which may conveniently be divided into six sections :—

1. A thicketed stretch of one and a-half miles from the Masai reserve to the Sigawa River (see Map). Above the Lolgorien-Kisii road, *Trichocladus ellipticus*, *Acacia stenocarpa*, *Syzgium cordatum* and *Pygeum africanum*, are the dominant trees. *Scutia buxifolia*, *Gymnosporia senegalensis*, *Carissa edulis* and *Croton dichogamus*, are the chief components of the sub-dominants and the undergrowth. The vegetation, as a whole, provides a dense, well-nigh impenetrable mass. Outside this riverine forest, scattered clumps of small, light thickets extend up the eluvial slopes on both sides of the Oyani River. Below the Lolgorien-Kisii road, the continuous band of the riverine forest becomes narrower and less dense ; the outer edges break into separate but long thickets, and *Trichocladus* disappears.

2. The Oyani supports only a very narrow belt of dense thicket from its junction with the Sigawa to a point half a mile below the Nyalich tributary ; but for this distance of about six miles, the vegetation appears, from the hillsides, as a cluster of close-growing, separated clumps of thickets (Plate XI, fig. 2). These large clumps occur on both sides of the river in this section and they comprise mainly *Parinarium curatellaefolium*, *Bridelia micrantha*, *Psychotria* sp., *P. africanum*, *Carissa edulis*, *Gymnosporia senegalensis*, *Rhus glaucescens* and *Toddalia asiatica*. The composition of the actual riverine bush is much the same as it is in the upper reaches, but low shrubs grow more profusely at the base of the larger trees. The vegetation widens at the junctions of the smaller streams and the Oyani, most of the former being clad with entangled shrubs along the greater part of their course.

3. A wide strip of country for about three miles starting from below the Nyalich, passing to the south of Rombe hill, to nearly a mile below where the Aram flows into the Oyani is covered partly by close scrub regenerating on old cultivated patches and partly by taller trees forming the nuclei of numerous small thickets. The low, shrubby thickets are made up of *Acacia pennata*, *Euchlea divinorum*, *Carissa edulis*, *Rhus glaucescens* and *Scutia buxifolia*. *Erythrina tomentosa* and *Combretum* sp. are dominant in the numerous other thickets but they are more frequently found on the eluvial slopes and in open country. In the bush on the river-banks are *Syzygium cordatum*, *Bridelia micrantha* and many *Ficus* sp. The wooded course of the Nyalich begins at a short distance above its junction with the Oyani and continues to the source of the former near the extensive forest of Angwe, which covers a large area in the north-east of Kanyamkago and also a large part of the adjacent location of Sakwa. It is near this forested area that the Nyarago rises and then takes a different direction round the north of Rombe hill to join the Oyani several miles down that river. The vegetation in the uppermost section of the Nyarago is not dense ; but it suffices as shelter for tsetses that might find their way to its vicinity. This line—Oyani-Nyalich-Angwe-Nyarago-Oyani—is of significance from a practical reclamation point of view. As will be noted later, it may serve as a convenient way for further dispersal of tsetses over the Kanyamkago location and into Sakwa. Both the section of the Oyani under consideration and this flank are crossed by the Suna-Kisii road over which there is a considerable amount of vehicular traffic. As on most of the tributaries, here also, thick bush provides suitable conditions for flies carried on lorries, cars, etc., to alight, to find shelter, and to increase the density of tsetses.

4. A stretch nearly four miles long on the Oyani from below the Aram stream to about a mile below the junction of the Nyarago and the Oyani. This section should perhaps be divided into an upper and a lower sub-section. In both, there are long patches of seasonal marshy ground on each side of the river ; and the fringe of dense forest is pushed away, as it were, from the river. The lines of vegetation in the upper section are very narrow, whereas they are much broader in the lower

section. An aerial picture taken below Uriri (Plate XI, fig. 2) clearly shows the spaces between the bush ; and it shows, incidentally, a large number of villages that have been abandoned. On the north of the Oyani, in this section, is that area which, according to the chief and other evidence, is being slowly depopulated by the invasion of tsetses. The dense wooding is somewhat like that on the Sigawa, and there are long stretches where the trees and shrubs form a tunnel-like passage through which the Oyani flows. The dominants are *Bridelia*, *Psychotria* and *Parinarium* ; but they are lighter and less robust than the same species higher up the river. The shrubs and creepers are *Euchlea*, *Scutia*, *Acacia pennata*, *Toddalia* and *Cissus* and *Asparagus*.

5. A comparatively open strip from near the Nyarago to about one and a-half miles from the Kuja River. For approximately four miles there are very few large trees on the banks of the river ; and the shrubby undergrowth is replaced by long coarse grass. There is a small number of thickets around the bases of the fig-trees, under the canopy of candelabra *Euphorbia* and the flat-topped *Acacia* trees. An occasional *Hyphaene* palm may also have a few shrubs to form a low thicket. The valley proper now widens ; and on the south of the river there are long vleis or marshes with several species of *Acacia*. The prevalent type is *A. usambarensis*. Between the vleis and the more open eluvial savannah, there is a belt of close-growing, stunted trees with *Combretum*, *Heeria*, *Erythrina* and *Parinarium* predominating.

6. A densely forested band for one and a-half miles before the Oyani meets the Kuja River. It contains the species already mentioned with the addition of a greater number of *Ficus* sp. and *Acacia campylacantha*. Here also there is a margin of *A. usambarensis*. At the confluence of the two rivers, the vegetation becomes heavier and dense, and spreads out in the shape of a fan.

The eluvial slopes in Kanyamkago support a rich growth of *Combretum* spp., *Heeria reticulata*, *Erythrina tomentosa* and *Parinarium curatellaefolium* and many other less common species. Patches of light thickets are distributed over the hillsides, while *Combretum* in particular occupies the larger areas of open country. In the small drainage lines, the bush extends up, and even over, the watershed between the Oyani and the Gori on the south and the Oyani, the Ougo and the Sari on the north. A glance at the accompanying map will indicate the possibilities of dispersal of flies over an extensive area in this region of South Kavirondo.

Tsetse-fly Infestation.

The writer (Lewis, 1937) stated in a publication on the tsetse-flies in the western (Ol Orokuti) section of the Masai reserve that " *G. palpalis* only was found on the Oyani (Kayan) River near the Masai-South Kavirondo border." Further, and more extensive, exploration indicated that *G. palpalis* in the uppermost reaches of the Oyani occurs seasonally, and then only in small numbers. It is also restricted to where the Lolgorien-Kisii road crosses the Oyani in Arambe. It is now evident that the species has not established itself in this section and that the specimens collected on the previous occasion had been conveyed from the Gori river basin ; or they may be a periodic expansion of the *palpalis* belt which enables the flies to spread beyond the watershed by way of the numerous streams which rise in the hills separating the Gori and Oyani valleys.

No flies or breeding-places were found actually inside the heavy bush on the Oyani above the Lolgorien-Kisii road. The atmosphere is extremely dank and rather cold. There is no opening or path to permit free movement for the tsetses. The ground is waterlogged or marshy in most places ; and where the soil is dry, it is hard underneath a layer of wet and mouldy humus.

Native patrols provided with hessian screens caught two *G. palpalis* and three *brevipalpis* on the outskirts of the riverine thickets ; but searches over a wide area for the puparia of these species were unsuccessful. *G. pallidipes* was more numerous though by no means abundant. It was always taken on screens when the patrol were moving between the light thickets scattered over the lower slopes of the hills. Close examination of likely breeding-places of *pallidipes* failed to produce puparia ; but, of course, not every thicket was searched. It appears, however, that while *palpalis* and *brevipalpis* have not yet found this particular section favourable as a " home " but capable of providing shelter and suitable as a hunting ground, *pallidipes* is likely to find a foothold and to create a focus for wider infestation. The last mentioned species obviously prefers the vegetational cover below the Lolgorien-Kisii road where the fly was more abundant and where many puparia were discovered in scattered bushes. The puparia were not very abundant, nor were the flies as common as they were below Uriri. The fly population can be said to be low, yet sufficient to render the pasturing of cattle precarious. *G. brevipalpis* seldom appeared to the screens. A few specimens were captured ; and a number of empty puparia were collected from the dense thickets outside the vegetation on the banks of the river. *G. palpalis* seemed to be absent from the stretch between the road and the Sigawa stream.

Only one *pallidipes* was obtained on the course of the Sigawa. The natives in a small village near by maintain that tsetses are more prevalent on the Oyani and Sigawa at the time of the long rains. They increase in numbers soon after the first showers and are actively on the wing for several weeks after the cessation of the wet weather. In the dry season they tend to disappear. The specimens collected during this short investigation—a dry period—seemed to seek the shade of clumps of thicket, especially where these were grouped together. The most fruitful time of the day was between 8.30 a.m. and 11 a.m. ; but a few flies ventured out into the open bush to where the camp was pitched about 400 yards from the Oyani River in the evening.

From the careful investigation into the suitability of the vegetation for harbouring tsetse-flies, the frequency and the distribution of breeding-places in this portion of the valley, it may be deduced that *G. pallidipes* and *brevipalpis* infest the area more heavily in some seasons than in others, and that during the favourable periods there is an effort to settle in it as a permanent haunt. It cannot be a safe place for cattle even in the dry season, as may be gathered from the presence of the fly during this survey. The extension of good vegetational cover in the tributary valleys assists more general dispersal. On the Manyonge—lower down the valley—puparia of *brevipalpis* and *fuscipleuris* were found in a relatively loose thicket ; and an adult of *pallidipes* was taken still further up that stream. There is hardly any doubt that the flies gain easy access to the Akok and Ngongo localities by this tributary.

Still further down the Oyani, a change takes place in the formation of the vegetation, soon after passing the Sigawa. The elongated marginal thickets sever into small series of separated clumps (Plate XI, fig. 2), while the bush on the river retains its gallery formation. It is in the clumps of bush that the larger tsetses find the best conditions for breeding. Puparia of *brevipalpis* and *fuscipleuris* were obtained in large numbers, but those of *pallidipes* were comparatively rare. *G. brevipalpis* and *fuscipleuris* do not larviposit indiscriminately throughout this vegetation ; they seem to have chosen many thickets which are more suited to their purpose than others which do not obviously offer better conditions. It was observed, however, that the most popular breeding-grounds, deduced from the numbers of puparia collected in these sites, were situated near the junction of the Oyani with its larger tributaries. There was always plenty of deep shade and good shelter provided by the luxuriant growth of trees and shrubs ; and there was adequate scope for free movement between the clumps and on the outskirts of the riverine forest. The selection of these localities may greatly be influenced by their convenience as resorts for flies retreating from the wider areas of dispersal in the dry weather.

Apart from the concentrated breeding-places, there were others in scattered thickets ; the number of puparia was usually low. The impressions of the fly-position in this section must be taken from the distribution of the puparia because, in the case of *G. brevipalpis* and *G. fuscipleuris*, adult flies were so scarce. They did not readily appear to the patrols. No bait-oxen were available ; and every other effort was made to attract the flies. It was near the river south of Ombo hill that trials were carried out to ascertain the most favourable period of the day to collect *brevipalpis* and *fuscipleuris*. For three days, routine patrols were conducted through the riverine bush, in between the thickets and along the margins of the dense vegetation. Trials were carried out at dawn, throughout the day, at dusk, and late at night. The catches were so low that no conclusions could be drawn.

Records were taken of the climatic conditions in three distinct types of vegetation, and though there was no correlation between them and the activity of the flies as observed during the three days, they are included here (see table p. 351) in order to show the approximate conditions prevailing at the time.

The records for three days are hardly sufficient to express any significant differences in the three positions. A longer series of observations would show, it is believed, that the early morning conditions varied in a different way from the day conditions. For the mid-day periods, the riverine thicket has a distinctly lower temperature and a higher relative humidity than those outside. There is very little difference between the margin of the riverine thicket and 200 yards outside. The saturation deficit within the riverine thicket is also somewhat lower than that outside.

It will be observed that *G. pallidipes* contrives to exist in this band of bush, and more flies of this species were collected than of the other two. It does not seem to have adjusted itself to the environment, but manages to deposit its young in scattered thickets.

Attention has already been drawn to the connection of the vegetation on the Oyani and the Nyalich. Its importance rests in the fact that there is an attempt on the part of *brevipalpis, fuscipleuris* and *pallidipes* to spread from the Oyani River up the Nyalich. All three species have been taken in the lower mile of the latter, and as its source is situated near the dense forest of Angwe, there is reason to fear that the flies may ultimately reach Angwe and infest the area permanently. Such importance was attached to this possibility that a special search was made later in Angwe. Only one *G. pallidipes* was obtained and the single specimen was captured in the centre of the forest. The few natives who reside in this part of the location, and others in the Sakwa location, say that they cannot keep cattle in the neighbourhood of Angwe because they die from the bites of tsetses—flies with which they are well acquainted. Their account of animal trypanosomiasis, the recognition of the insect vector, and their reports of the seasonal incidence of both, have to some extent been verified.

An investigation of the Nyarago, which rises near Angwe forest, failed to reveal the presence of tsetse-flies other than an occasional *G. palpalis*. On the first search, one specimen was taken in the wooded ravine about a mile from the junction of the Nyarago and the Oyani. Later, two specimens were collected near a bridge over the Nyarago about five miles up-stream. It will be appreciated that the presence even of one or two *palpalis* on this river is difficult to explain, for there appears to be little inducement for this species to range up the sparsely wooded lower reaches of the Oyani and then to venture over an open stretch of about a mile on the Nyarago. The existence of the fly, however, does show that the Nyarago-Nyalich flank needs to be considered in any scheme of reclamation in Kanyamkago. It is not known what connection there is between the Auchombe stream and the Angwe forest. Indeed, the eluvial slopes on both sides of the Oyani River are so provided with stream-beds that the vegetational cover may easily be utilised by all species for seasonal dispersal. The dry-weather conditions seem to drive the tsetses back into the more humid valley of the Oyani itself.

OYANI RIVER VALLEY :—ALT.=4,600 FEET ; POSITION=34°30′×0°59′S.

Date		Time	Within riverine thicket					At margin of riverine thicket					Outside (200 yds.) riverine thicket—open area					Cloud	Notes
			Dry temp. °F.	Wet temp. °F.	Per cent. Humidity	Dew Point °F.	Sat. Deficit	Dry temp. °F.	Wet temp. °F.	Per cent. Humidity	Dew Point °F.	Sat. Deficit	Dry temp. °F.	Wet temp. °F.	Per cent. Humidity	Dew Point °F.	Sat. Deficit		
1.viii.37	...	18·40	69	66	86	—	·008	—	—	—	—	—	70	63	70	—	·008	8/10	Darkish
2.viii.37	...	08·45	67	63	81	—	·005	65	62	86	—	·007	—	—	—	—	—	5/10	
,,	...	12·00	78	65	52	60	·011	82	69	54	65	·012	82	68	51	64	·012	3/10	
,,	...	14.00	81	65	45	59	·012	86	71	50	67	·013	85	67	41	61	·014	1/10	Wind rising
,,	...	16.00	75	65	60	61	·010	82	67	48	62	·012	83	66	43	60	·012	4/10	
,,	...	18.00	72	68	83	67	·009	75	66	64	63	·010	74	64	60	60	·009	5/10	
,,	...	18.45	—	—	—	—	—	—	—	—	—	—	68	62	73	—	·007	dark clear ?	
,,	...	19·45	—	—	—	—	—	—	—	—	—	—	62	60	90	—	·005	—	
4.ix.37	...	07.00	59	56	84	55	·005	60	57	85	56	·005	63	58	76	55	·006	—	
,,	...	08.00	73	63	60	59	·009	74	64	60	60	·009	76	64	54	59	·010	—	
,,	...	10.00	82	69	54	65	·012	83	66	43	60	·012	83	69	51	65	·012	1/10	
,,	...	12.00	85	71	52	67	·014	86	69	44	63	·013	84	64	35	56	·014	3/10	
,,	...	14.00	73	69	83	68	·009	72	67	78	65	·009	76	70	75	68	·010	7/10	
,,	...	16.00	77	68	65	65	·010	78	68	62	65	·011	85	67	41	61	·014	—	Slight shower on hill
,,	...	18.00	72	66	74	—	·009	71	67	82	—	·009	—	—	—	—	—	—	
5.ix.37	...	07.00	60	58	90	57	·005	62	60	90	59	·005	64	61	85	60	·006	—	
,,	...	08·00	70	63	70	61	·008	73	65	67	62	·009	72	65	70	63	·009	1/10	
,,	...	10.00	78	68	62	65	·011	77	67	62	64	·010	78	69	65	66	·011	1/10	
,,	...	12.00	86	70	47	65	·013	84	68	46	63	·014	85	69	47	64	·014	1/10	
,,	...	14.00	86	71	50	67	·013	84	70	62	71	·014	83	71	57	67	·012	—	
,,	...	16.00	78	69	65	66	·011	78	69	65	66	·011	77	68	65	65	·010	—	Thunder shower
,,	...	18.00	70	67	86	66	·008	70	67	86	66	·008	69	67	91	66	·008	—	Clearing up

The area from about a mile east of the Suna-Kisii road to the Aram stream below Rombe hill is one that brings to mind the type of country generally infested with *G. pallidipes*. It is an area where there are still a few occupied villages, but where numerous cultivated plots have been abandoned and many villages deserted. On the old cultivated land and around the huts dense shrubs have grown to form convenient shelter for tsetses wandering from the heavier, riverine forest. Along the river-banks there are open areas of seasonal swamps and extensive patches of bush which render the riverine forest less compact than that higher up the Oyani. *G. pallidipes*, *brevipalpis* and *fuscipleuris* occur in this section also ; but *pallidipes* is definitely most prevalent. The other two species, while not uncommon, are not so abundant ; they manage to find a few isolated spots in which to breed. *G. pallidipes* is much more at home, and, from evidence of catches by screen, spreads over a wide area. Its breeding-places also are widely scattered in the light thickets on the hill-slopes, near the river and in the expanse of bush on the Aram stream. Several *pallidipes* were taken on the main road and on the native tracks in the vicinity of this Suna-Kisii road. Natives arriving at Rombe camp invariably brought a specimen that had followed them from the valley.

It was near the Oyani bridge that a few *G. palpalis* were caught by the fly-boys. An examination of the bush on the Sigara River which follows the line of the road, and of other likely habitats, failed to show the existence of puparia of this species. In this instance again, it is felt that *palpalis* was, and is, conveyed on vehicles from the Gori valley. One of the two important stock-routes passes over this bridge. The herds may well bring following flies from the Gori area.

The chief of Kanyamkago lives on Uriri hill and he was much interested in the investigation carried out at his instigation. He spoke of the location, its history, the people, and how many of them had left the larger part of Kanyamkago because of the heavy losses from animal trypanosomiasis, followed by their inability to pay the hut-tax. He explained how it was that the tsetses were gradually reducing the cattle in Nyakororo (west of the Nyarago) and that the diagnosis of the disease had been confirmed at the laboratory. In his little village area he could not keep cattle on account of the fly ; and he felt that some measure of control would encourage his people to remain in the location and assist in the undertaking. The people were prepared to subscribe to a scheme of reclamation that would enable them to improve their standard of living and provide them with the means of producing better food for consumption.

No tsetse-flies were found in that section of the Oyani, from just below the Aram stream to the end of the bush a short distance lower down than the Nyarago. An intensive search was made in view of evidence of the evacuation of an area—Nyakororo —on the north of the Oyani. The failure to find fly forces one to consider this section as an area of fly-dispersal only. But the presence of isolated specimens of *G. palpalis* on the Nyarago itself suggests an attempt on the part of the tsetse to persist in the most densely wooded spots throughout the year ; and the discovery of one empty puparium of *pallidipes* lends a little weight to this belief.

The question arises as to how does *G. palpalis* reach the Nyarago ? Does it spread up the Oyani, which, it will be noted later, is devoid of good vegetational cover for the greater part of its length from a short distance below the Nyarago to within one and a-half miles of the Kuja river ? Or have the few specimens collected reached the Nyarago from the main road ? There is the possibility of their having been carried by natives trekking from the Kuja. The uncertainty of these explanations does not diminish the importance of the actual existence of this species, nor the danger of the Nyarago-Nyalich flank.

No tsetse-fly was caught, nor puparia found, on the lower region of the Oyani until that strip of forest was reached about one and a-half miles from the junction of the Oyani and the Kuja Rivers. It has already been stated that the riverine bush disappears here. The valley opens out, becomes more flat; and the steeper acclivities of the catchment area are replaced to some extent by open vleis which give way to open savannah. There is extremely little cover for flies to breed; and during the dry seasons, adult flies would hardly venture to move up even near the river.

Although there are native villages on the south side of the river as well as on the north, there is evidence of the population in the former moving out of the area because of tsetses. The inhabitants say that tsetses do exist on the Oyani in the months of April and May, but the flies that worry them most appear from the smaller streams. The Osogo River, they claim, is seasonally infested with tsetse-flies that come from the Nyamage range of hills.

A brief examination of these hills and streams confirmed the presence of *G. pallidipes* and *G. palpalis*. These species were found on the Eko and Nyaronge streams, tributaries of the Gori. No fly was found on the Osogo, the Ongora, or in the Kodili locality; but from the character of the area and the vegetation, there is no reason to believe other than that the flies do disperse over a considerable portion of the area.

On the north side of the Oyani, the people do not usually build their huts near the river except a few who cannot resist the desire to fish in the Kuja. Most of the natives have learnt from experience, or by advice, that the danger of human trypanosomiasis can be reduced or eliminated by such precautions. The hinterland, as it were, is densely populated; it constitutes one-quarter of the location where cattle are concentrated.

Before proceeding to deal briefly with the lowest section of the Oyani, reference may be made to an extension of the survey to include the Lasi, the Nyangina, the Minyera and the Ougo tributaries of the Kuja River. The first three are shallow hollows rather than streams; but in the rainy season water flows in these channels. There is no riverine vegetation that may be utilised by tsetses moving from the infested area of the Kuja. The Ougo penetrates far into Kanyamkago and is provided with a moderate amount of thickets. Although no fly was actually collected during the survey, it is said to harbour the flies in small numbers when the rains are on. There is no evidence of any serious spread of *G. palpalis* or any other species of tsetse.

The last stretch of the Oyani is heavily infested with *palpalis* for a distance of one and a-half miles before that river enters the Kuja. None of the other species was found. Even in the dense wooding on the Kuja in Kanyamkago where one would have expected to find *brevipalpis* and at least a few *pallidipes* or their puparia, no species other than *palpalis* could be obtained.

The importance of the *palpalis* infestation may be assessed by the existence of several cases of trypanosomiasis among the natives and by the density of the flies which, if increased in more favourable seasons, would result in wider dispersal of the species.

The problem of reclamation of the fly-infested areas in Kanyamkago is complicated by the presence of four species of tsetses. Their habits, as far as they are known, differ and require further study on which to base appropriate measures of eradication.

Clearing all the natural bush on the rivers, numerous stream-beds and eluvial areas is uneconomical and undesirable—especially in hilly country; and the cleared land must be maintained free from rapidly regenerating bush or protected from re-infestation.

Partial or discriminate clearing by destroying thickets and thinning-out dense forests should so change the environment as to affect the fly-population adversely. The degree to which partial clearing should be carried out depends on a thorough knowledge of the biology and the adaptability of each species of tsetse in the particular region and on systematic trials on the effect of such clearings. By reducing the vegetational cover only in the permanent haunts, or dry weather retreats, of the species, labour and time may be saved ; but this can be achieved only after a very detailed survey or a sound knowledge of the behaviour of the flies under different environmental conditions.

The " densification " of bush by releasing the vegetational succession, or by planting, may be applicable to *C. pallidipes* in the Oyani Valley ; but in the process it might serve to extend the infestation by *brevipalpis*, *fuscipleuris* and *palpalis*. It would be extremely difficult to create an efficient, unbroken belt of dense forest across the valley.

Trapping is useful against *G. pallidipes* ; less effective in the case of *palpalis*. No trap has yet been devised which can be said to be of practical value against *brevipalpis* and *fuscipleuris*.

Hand-catching helps to reduce *palpalis* and *pallidipes* in isolated blocks of infested wooding ; but it is not very successful with *brevipalpis* for which bait-oxen are usually necessary to attract the adults. Very little is known about *fuscipleuris*.

It seems clear that no one method of control, except complete destruction of forests, can yet be employed in such a mixed fly-belt with a definite assurance of success. Even in areas where only one species exists or where there are two whose habits are approximately alike, the control measures adopted have, of necessity, to be extended over a period of years. In other words, the reclamation of tsetse-infested areas is a slow process In the case of the Oyani Valley, it is felt that a comprehensive scheme of progressive development and settlement may be put into operation. It should provide for the conversion of tsetse-infested localities into productive cultivated land, improved pastures and even groves and parks. As the tsetses are reduced and driven back—and the area protected from re-infestation—stock can be introduced behind the advance line of cultivation. Later, the indigenous bush could be permitted to regenerate along the river-banks and assume its natural climax.

By such a scheme, not only will land be regained from tsetses, but opportunities will occur to improve native agriculture and stock, increase production and raise the standard of living in native reserves.

Breeding-places of Glossina fuscipleuris.

As *G. fuscipleuris* is usually found in dense, riverine thickets or in dense forest, it is obvious that the fly should select its breeding-place in or near such vegetation. The existence of the species in the Oyani Valley naturally led to searches for puparia and a study of the localities which appeared most favourable to larviposition. It was a few hundred yards above the bridge over the Oyani, opposite Uriri hill, that three different kinds of full puparia were collected by the author in September 1937. Two were readily recognised as those of *pallidipes* and *brevipalpis*. The third belonged to none of the known species of *Glossina* in Kenya Colony, but it resembled that illustrated (Austen & Hegh, 1922) as the puparium of *fusca*. The close resemblance of *fuscipleuris* and *fusca* and the presence of the former in the Oyani Valley indicated that the third type of puparium might well belong to *fuscipleuris*. It was clearly desirable to confirm the supposition. More puparia were collected, several of which were reared. The adult flies were examined after emergence and proved to be *fuscipleuris*.

The first collection of puparia was obtained at the base of a large fig-tree in the riverine forest and about ten yards from the river-bank. The specimens were found together with puparia of *brevipalpis* and *pallidipes*. The site was typically that where *brevipalpis* often occurs.

The breeding-places of *G. fuscipleuris* have not hitherto been described. A detailed account of a few typical sites in the Oyani Valley may be of interest. In addition to the original site already mentioned, many places were located where the number of *fuscipleuris* puparia did not exceed three or four. One of these was an isolated thicket about twenty yards outside the riverine bush on the Manyonge. It was approximately forty yards in circumference ; it contained two large trees—*Parinarium curatellaefolium* and *Bridelia micrantha*—forming a canopy over a loose entanglement of undergrowth, comprising slender *Pygeum africanum*, *Psychotria* sp., *Gymnosporia senegalensis* with *Euchlea divinorum*, *Carissa edulis* and *Rhus glaucescens*. The ground within the thicket was sparsely covered with grass, which at the periphery was tall and formed a dense fringe. It was just inside this peripheral fringe, and in dry, slightly friable soil, that four empty puparia were found. Two belonged to *brevipalpis* and two were those of *fuscipleuris*. The thicket was not dense and seemed to be not highly favourable to either of the two flies.

Later experience of the breeding-places of *G. fuscipleuris* indicated that this particular spot—and many similar places in the valley—were not much frequented for larviposition. The case serves as an illustration of the ability of both *fuscipleuris* and *brevipalpis* to utilise comparatively light thickets for depositing their young. Puparia of *brevipalpis* have been found in similar situations far from rivers in other fly-belts in the Colony. It may be deduced that such places are used only when environmental conditions outside the forests permit increased activity and wider dispersal. The distribution of these temporary breeding-places shows the ranging tendency of the species.

Clumps of dense thicket provide more suitable conditions for breeding as manifested by the number of puparia collected in them. Most of the favoured clumps were nearly impenetrable to man ; and the interior was heavily shaded and damp. The photograph (Plate XI, fig. 2) shows a section of the valley with large numbers of these thickets. Plate XI, fig. 1 is an aerial view of a longer stretch of another section ; it shows the relatively narrow band of dense bush and the open nature of the eluvial savannah of *Combretum*. An isolated thicket was penetrated after cutting away a tangled mass of branches and creepers, the grass being thick and tall outside the thicket. In an area of a yard square, 38 puparia of *G. brevipalpis* and 48 puparia of *G. fuscipleuris* were found. The majority were empty shells, while a number were full puparia. The ground was covered with weeds belonging to the genera *Commelina* and *Justicia* or *Isoglossa*. The soil was a light loam, very friable and moist, with a surface covering of humus of about an inch deep. The composition of this thicket was much like that described above but for the absence of *Parinarium curatellaefolium*, and its greater density. *Bridelia* formed the dominants ; *Rhus*, *Pygeum* and *Gymnosporia* were the main constituents of the sub-dominants, which were interlaced with the more slender branches of *Scutia*, *Euchlea* and the creepers *Cissus* and *Euphorbia*.

Another similar thicket, about a hundred yards from the Oyani, produced 50 puparia of *G. fuscipleuris*, 36 puparia of *brevipalpis* and one puparium of *pallidipes*.

All breeding-places of *fuscipleuris* and *brevipalpis* were close to, or connected with, the heavy forest of the Oyani or its tributaries.

The Puparium of Glossina fuscipleuris.

The puparium of *G. fuscipleuris* is very much like that of *fusca*. The latter tapers towards the posterior and is more egg-shaped than the former, which is more regularly oval.

The length of the puparium of *G. fuscipleuris* is from 7·5 to 8·0 mm. ; its greatest width from 4·25 to 4·50 mm. ; the posterior lobes, or tumid lips, vary in length from 1·35 to 1·56 mm. The notch, when examined from the dorsal plane, is usually cup- or U-shaped ; but when viewed from below, it is more like a V in the majority of specimens ; ventrally it is deeper, measuring from 0·78 to 1·00 mm., dorsally it is from 0·62 to 0·84 mm. deep ; the width of the notch ranges from 0·44 to 0·62 mm. The dorsal, inner edges of one or both lobes sometimes bend inwardly at the distal end, giving the notch a slightly hooked appearance. This tendency is also shown in one of the lobes of the puparium of *fusca* illustrated by Austen & Hegh (1922). The ventral, inner edges of the lobes in *G. fuscipleuris* are definitely V-shaped in the anterior third. They then curve outwards to form a concavity which ends in a more prominent hook, giving the notch when examined under the binoculars the appearance of a pair of calipers. A side view of the lobes shows how the dorsal inward projection presents a flattening of the posterior end, whereas a posterior view of the stigmatic cavity shows clearly the position of the prominences.

It would be of interest to compare the ventral notch and the posterior opening of the stigmatic cavity of the puparia of *fuscipleuris* and *fusca*. There is a considerable difference in the shape and size of this opening as seen in an end view of the puparia of *Glossina* in Kenya Colony.

A Parasite of G. fuscipleuris and G. brevipalpis.

A large number of full puparia of both these tsetses was collected in the Oyani Valley in August and September 1937. Numerous puparial shells also were collected, and many of these were complete but for a tiny hole indicative of natural parasitization by *Syntomosphyrum glossinae*, Wtstn. A few of the puparia had holes that resembled those made by the parasite *Stomatoceras micans*, Wtstn., while others showed that normal emergence of the tsetse had taken place.

A rough estimation of parasitization by the *Syntomosphyrum*-like insect was *G. brevipalpis* 45 per cent., and *G. fuscipleuris* 20 per cent.

The full puparia were taken to the experimental station in the Lambwe Valley, South Kavirondo, in order to rear adults of *G. fuscipleuris* and to breed any parasites that might emerge from puparia of this tsetse and puparia of *brevipalpis*. Parasites emerged from two batches of puparia put into glass tubes. They were Hymenoptera of the family PROCTOTRUPIDAE. Specimens were sent to the Imperial Institute of Entomology, where by courtesy of Sir Guy A. K. Marshall they were identified as *Trichopria capensis*, Kieff., var. *robustior*, Silv.

This insect was first found as a parasite of the puparium of a tsetse by Harris (1930) who collected it in 1923 from *G. pallidipes* in Zululand. Nash (1933), in his observations on the breeding of *Syntomosphyrum glossinae*, refers to the appearance of *Trichopria* which parasitized the puparia of blow-flies before they (the puparia) were given to *Syntomosphyrum*. He adds that the *Trichopria* was useless, as it would not attack the puparia of *G. morsitans*. Harris states " Two of the females (*Trichopria*) were seen to attempt to parasitise *Glossina* puparia which were given them, but there was no result. I have only met with these parasites on this one occasion."

The preliminary observations with material from the Oyani Valley were carried out a week or so before the author's departure on home leave. Mr. W. P. Langridge, Tsetse-fly Overseer in the Lambwe Valley, was requested to collect further material and to conduct a few experiments in rearing *Trichopria* by the blow-fly method discovered in the Department of Tsetse Research, Tanganyika ; and to test the ability of the *Trichopria* to parasitize puparia of *fuscipleuris*, *brevipalpis*, *pallidipes* and *palpalis*.

The following remarks have been extracted largely from Mr. Langridge's report. Parasites were obtained from several puparia of *G. brevipalpis* and *fuscipleuris*, and from one *pallidipes* collected in the Oyani Valley. Of 24 puparia of *brevipalpis* put together in one glass tube, a cluster of *Trichopria* emerged from one. It was not known that the brood would attack the other puparia within a few hours after emerging. Such, however, was observed to be the case, with the result that only four adult tsetses hatched out. Fourteen of the puparia failed to hatch and five produced broods of the parasite. Eight of the unhatched puparia were dissected under a binocular microscope. Five of these contained a mass of yellow cocoons, some of which were ruptured apparently to release the adult *Trichopria* parasites. Two appeared to have been attacked by a mould which had reduced the contents of the puparia to a cheesy mass ; the last puparium contained a normal pupa of *brevipalpis*.

It is unlikely that the first brood of parasites was wholly responsible for the parasitism in the other ten puparia containing *Trichopria*. The puparia were collected in the Oyani Valley where natural infection was known to exist. Two female *Trichopria* were actually observed to puncture the puparial shell with their ovipositors.

Fifteen puparia of *G. fuscipleuris* were also put into tubes, precautions now being taken to prevent contact with the parasites on emergence. Two adult tsetses hatched out, five produced parasites and eight failed to hatch.

Further trials were conducted to confirm the ability of *Trichopria* to parasitize puparia of tsetses and to ascertain whether it had any preference for a particular species. Adopting the technique employed in Tanganyika, large quantities of the parasite were raised from puparia of *Chrysomyia chloropyga*, a common blow-fly in the Lambwe Valley. Twenty parasites were put into a tube containing a tsetse puparium. The following table summarises the result ; but it is to be noted that fourteen of the puparia of *brevipalpis* and all the puparia of *fuscipleuris* were collected from the Oyani Valley. The other specimens were obtained in the Lambwe Valley, where no *Trichopria* have yet been discovered despite diligent search.

Species	No. of puparia	Tsetses emerged	Parasites emerged	Attacked by mould	Did not develop
G. brevipalpis	38	4	26	2	6
G. fuscipleuris	14	2	11	1	0
G. pallidipes	15	5	1	6	3
G. palpalis	358	176	0	26	136

Females of *Trichopria* were again observed attacking many of the puparia of *fuscipleuris* and *brevipalpis* ; and although some of those puparia collected in the Oyani may have been parasitized before the test was undertaken, there is no doubt that *Trichopria* can successfully penetrate the puparia of tsetses. It does not appear to favour the puparia of the smaller tsetse-flies but shows a predilection for the larger species. This preference is not evinced in the case of blow-fly puparia, for it attacks both the large and the small equally readily.

It was thought that the parasite attacked only those tsetse puparia whose contents had disintegrated owing to the action of moulds or bacteria. Dissection of 20 specimens sent to the author showed that this was not the case, so far as could be judged from the condition of the puparial contents and fragments of the undeveloped tsetse. It was discovered also that at times the parasite itself may fail to emerge, for in many instances batches of about fifty *Trichopria* were taken from puparia which had not produced adult tsetses or live parasites.

The development of *Trichopria capensis* var. *robustior* has not been studied in detail. Mr. Langridge, who is now engaged in this work, has ascertained that the life-cycle varies from 18 to 25 days. The adult lives, under artificial conditions, for about 10 days, and is readily killed by exposure to direct sunlight.

The parasites emerge from the puparia through one or more small holes that are very much like those made by *Syntomosphyrum glossinae*. With *Trichopria*, the holes are usually larger and the edges more jagged.

As a final observation, it may be stated that efforts to obtain a description of *Trichopria capensis* var. *robustior* have raised a doubt as to whether Silvestri actually described the variety or merely gave it a name with the intention of describing it later. Specimens have been sent to England for further examination and description, if necessary.

Acknowledgments.

The author gratefully acknowledges the assistance of Sir Guy A. K. Marshall, C.M.G., F.R.S., in the identification of the *Trichopria* and in arranging for the photographs of the puparia of *G. fuscipleuris* by the authorities of the British Museum (Natural History); of Dr. O. W. Richards, Imperial College of Science, London, for advice on the parasite; and of Mr. W. P. Langridge in conducting the preliminary experiments at his station in the Lambwe Valley.

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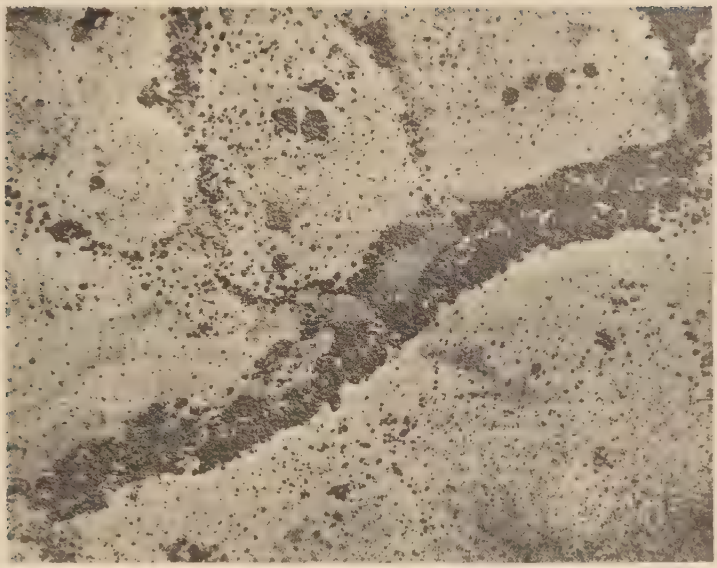

Fig. 1. An aerial view of the Oyani river forest, south-east of Uriri hill. (Reproduced by courtesy of the Aircraft Operating Co. of Africa (Pty.) Ltd., Johannesburg).

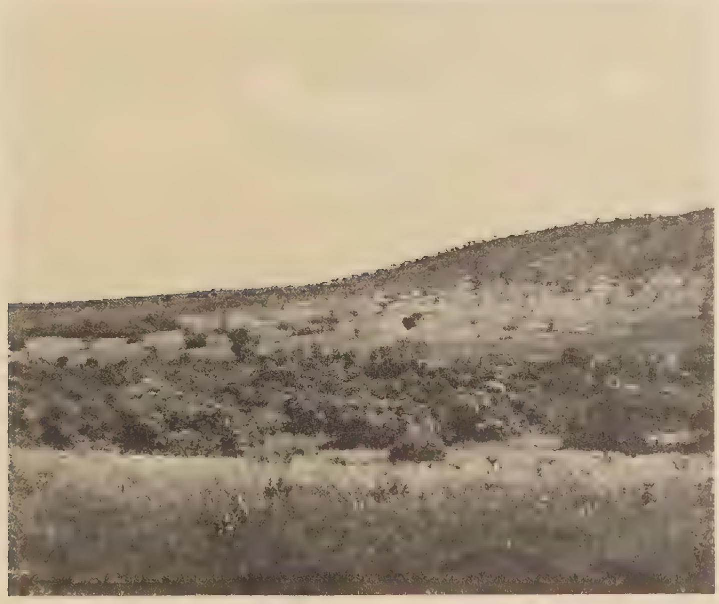

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Fig. 2. The home of *G. fuscipleuris* on the Oyani river, south of Ombo hill.

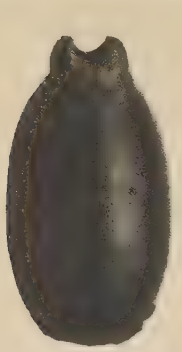

Fig 1. Dorsal view.

Fig. 2. Side view.

Fig. 3. A view of the posterior stigmatic cavity.

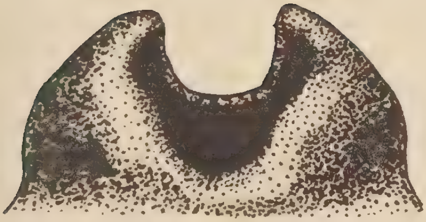

Fig 4. Ventral view of posterior notch.

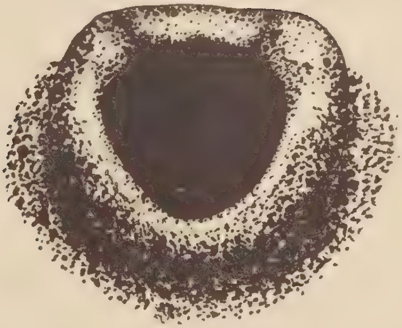

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Fig. 5. Oblique view of the stigmatic cavity.

THE PUPARIUM OF *GLOSSINA FUSCIPLEURIS.*

NEW INJURIOUS CURCULIONIDAE FROM SOUTHERN AFRICA.

By Sir Guy A. K. Marshall.

(Plate XIII.)

The types of the following new species have been deposited in the British Museum (Natural History).

Subfamily Brachyderinae.

Tanymecus rapax, sp. n.

♂♀. Derm piceous, with very variable grey and brown scales, not forming any definite pattern, usually the brown scales predominating, but sometimes the grey; the scales on the elytra broader and longer than usual, fairly dense but not entirely concealing the derm.

Head with coarse, longitudinally confluent punctures which become small and round on the vertex; forehead gently convex transversely, without any median fovea or carina, set with curved subrecumbent scales; eyes short oval, a little shorter than the rostrum (without the mandibles), moderately convex, about twice as long as the temples. *Rostrum* short, a little broader than long, as long as the head, very slightly narrowed from base to apex; the dorsum convex longitudinally and quite flat transversely, with the punctures smaller than those on the forehead and not longitudinally confluent, without any median carina, the apical area not abruptly declivous and without any metallic scales. *Antennae* red-brown; the scape reaching the hind margin of the eye; the funicle with joint 1 as long as 2+3, 2 shorter than 3+4, 3–6 subequal and about as long as broad, 7 a little longer. *Prothorax* slightly longer than broad (♂) or slightly broader than long (♀), rounded laterally, broadest at about the middle, of equal width at base and apex, the apical margin somewhat oblique in lateral view; the dorsum with small dense punctures without any smooth median line. *Elytra* rather narrow, parallel-sided from behind the sloping shoulders to beyond the middle, jointly sinuate at the base and jointly rounded at the apex, the striae rather deep, closely punctate and clearly visible through the scaling, the intervals even and finely rugulose, without any trace of posterior calli or subapical impressions; the scales much longer than in any of the known allied species and not closely appressed, becoming suberect on the posterior declivity, the setae squamiform and not distinguishable from the scales. *Legs* piceous, with rather sparse uniform grey scaling; the front femora scarcely thicker than the others and without long hairs beneath in ♂; the hind tarsi with joint 1 as long as 2+3, and 2 and 3 subequal. *Venter* with sparse narrow grey scales and numerous subrecumbent setae; ventrite 5 of ♀ shallowly impressed and almost bare in the middle.

Length 5·5–6·0 mm., breadth 1·8–2·0 mm.

S. Rhodesia: Hartley, 5 ♂♂ 4 ♀♀, xii.1938 (*A. Cuthbertson*).

Reported as damaging maize seedlings.

Most closely allied to *T. destructor*, Mshl. 1920, which occurs further to the east round Salisbury and Mazoe and is a larger insect, with the rostrum more narrowed apically, with confluent punctation and an abbreviated median carina; joint 2 of the funicle is much longer; the elytra are subtruncate at the base, with the shoulders more sloping, the apices divergent, and the scales much smaller; in the ♂ the anterior pairs of femora bear long erect hairs beneath.

Subfamily OTIORRHYNCHINAE.

Sciobius mordax, sp. n. (Plate XIII, figs. 3, 5).

♂♀. Derm red-brown, with sparse minute narrow pale scales above ; prothorax with an ill-defined median stripe of larger whitish scales, the pleurae densely clothed with still broader whitish scales ; elytra with the following markings of similar scales : an oblong scutellar patch, a sparser lateral stripe covering the whole side from the margin to stria 6, a sinuous band across the top of the declivity, and some irregular markings on the apical area ; underside with fairly dense pale scaling, except on the last three ventrites, where the scales become more sparse and setiform.

Head with the shallow punctures longitudinally confluent and often with an indistinct ridge above each eye ; eyes moderately convex and highest behind the middle. *Rostrum* as long as broad, with the sides almost straight, the genae not projecting, the base broadly arcuate ; the dorsal area broadly depressed in the middle, with an abbreviated low fine median carina, the lateral carinae parallel in ♂, but distinctly curving inwards posteriorly in ♀; scrobes unusually broad and deep, strongly curved, the longitudinal prominence in front of the eye well marked. *Antennae* long and slender, piceous, with sparse grey pubescence ; scape subcompressed, gradually clavate, deeply sinuate on the posterior edge ; funicle with joint 3 much longer than 1 but very slightly longer than 4. *Prothorax* tranverse, the median length a little more than half the basal width, the apex sinuate and the base broadly arcuate, hardly more transverse in ♀ than in ♂, the dorsum with fairly dense low shiny granules and a deep curved longitudinal impression on each side ; ♂ with the sides more strongly rounded in the anterior half and there about as broad as at the base, the basal angles being rectangular ; ♀ with the sides less rounded anteriorly and there narrower than at the base, the basal angles being distinctly acute. *Elytra* of ♂ narrowly ovate, widest at the middle, with the basal angles projecting beyond the base of the prothorax, somewhat flattened on the disk, with broad striae containing large close punctures, the intervals (except 2) rather narrower than the striae, finely rugulose with low flattened granules on the posterior declivity only, a few on intervals 3, 6 or 7 being more prominent ; elytra of ♀ much broader, more strongly rounded laterally and more convex dorsally, with the basal angles not projecting beyond the prothorax, the intervals much broader than the striae, in which the punctures are usually separated by flat shining granules, stria 9 being nearly always deeper in the middle than the others. *Legs* red-brown, with sparse grey pubescence ; hind femora of ♂ with a short carina at the base of the lower edge on the inner face, those of ♀ with small flattened granules on the inner face ; front tibiae of ♂ more slender and much less curved at apex than those of *brevicollis*, Fhs., shaped like those of *bistrigicollis*, Boh., but narrower.

Length ♂ 5·0–5·5 mm., ♀ 5·5–6·5 mm. ; breadth ♂ 2·5–1·7 mm., ♀ 3·7–6·5 mm.

NATAL : North Shepstone, 6 ♂, 9 ♀, ii.1939 (*E. F. Wright*).

Reported by the Division of Entomology, Pretoria, as damaging leaves of litchi trees.

Very closely allied to *S. brevicollis*, Fhs., which differs in having the rostrum a little longer than broad and the scrobes much narrower, the ♀ differing also in having the lateral carinae on the rostrum parallel ; joint 3 of the funicle is much longer than 4 ; the prothorax is much more transverse, with the sides regularly rounded and the basal angles obtuse ; the front tibiae of the ♂ are broader and much more strongly curved at the apex.

S. bistrigicollis, Boh., also much resembles the new species in general appearance but may be readily distinguished by the form of the rostrum, in which the genae are laterally dilated, especially in the ♂.

Glyptosomus angulatus, sp. n. (Plate XIII, fig. 1).

♀. Derm piceous, with dense greyish brown scaling and variable indefinite paler and darker markings, the paler scales with opalescent reflections.

Head with a prominent tubercle above each eye bearing a tuft of broad erect scale-like setae, the forehead concave with a shallow median sulcus ; eyes rather small, convex, placed rather low on the sides of the head. *Rostrum* as broad as the head without the eyes, slightly transverse, parallel-sided ; the broad dorsal area shallowly depressed down the middle with a mere trace of a low squamose median costa, the raised lateral margins parallel and bearing only a few recumbent scale-like setae. *Antennae* with the scape gradually clavate ; funicle with the two basal joints equal, 3 slightly longer than 4, 4–7 subequal and a little longer than broad. *Prothorax* transverse (2 : 3), slightly rounded laterally, broadest behind the middle, constricted at the apex, shallowly bisinuate at the base, with the basal angles rounded ; the dorsum with coarse punctures, which are mostly concealed by scaling, and a broad median sulcus, with two small tufts of short scale-like setae on the apical margin. *Elytra* sub-oblong, jointly sinuate at the base, with the alternate intervals costate and the suture obtusely raised on the posterior half, the costa on interval 5 terminating abruptly at the top of the declivity in the form of a large obtuse prominence, that on interval 7 forming a broad lateral projection at the base like a false shoulder, interval 9 with a conical prominence behind this humeral projection and exceeding it laterally ; the striae shallow, the contained punctures almost entirely concealed by scaling ; the raised intervals with multiple rows of recumbent scale-like setae. *Legs* piceous, with dense brown scaling and an indefinite paler patch on the femora ; tibiae with an additional small tooth adjoining the mucro at the apex, the corbels of the hind pair broadly enclosed.

Length 3·5–5·0 mm., breadth 2·0–2·7 mm.

ZULULAND : Mposa, 2 ♀, ii.1939 (*A. Tidboald*).

Reported by the Division of Entomology, Pretoria, as feeding on the leaves of litchi trees.

Nearly allied to the only other known species, *G. costipennis*, Lac. 1863, from Natal, which appears to be very rare in collections. The latter is very similar in general sculpture but is narrower ; the dorsal area of the rostrum is much more deeply impressed and its lateral ridges bear a dense row of broad erect setae ; joint 1 of the funicle is distinctly longer than 2 ; the sides of the prothorax are shallowly sinuate, so that the posterior angles project obtusely ; and the suture is much more strongly raised on the declivity.

Lacordaire put the genus at the end of his Peritelides, while admitting that it seemed out of place. He had clearly overlooked the fact that the corbels of the hind tibiae are broadly enclosed, and according to his classification it should come in his Oosomides next to *Cycliscus*, Schönh., to which it is evidently related.

Lalagetes edax, sp. n. (Plate XIII, fig. 2).

♂♀. Piceous to red-brown, with dense scaling concealing the derm ; prothorax pale brown, with three very indistinct narrow paler stripes ; elytra with very variable irregular mottling of brown and grey scales, the latter with an opalescent reflection.

Head with rugose punctures and a short frontal stria, but these entirely hidden by scaling ; forehead flat, widening behind ; eyes more convex than usual, highest behind the middle. *Rostrum* separated from the head by a strongly angulated furrow, parallel-sided, as is the broad median area, which is almost flat with a concealed median sulcus on the apical half ; the scrobes entirely visible from above, continuing shallowly up to the eyes. *Antennae* with the scape slender at the base, gradually clavate apically, strongly sinuate in the basal half, and set with long erect clavate setae ; funicle with joint 1 longer than 2, 3–7 subequal, slightly longer than broad. *Prothorax* transverse (3 : 5), rounded laterally, widest at one-third from the base, broadly but shallowly constricted at the apex ; the dorsum smooth, the rugulose punctures entirely hidden, and set with erect blunt setae. *Elytra* broadly oval, widest at the middle, jointly sinuate at the base, broadly rounded behind, the very slightly obtuse elevation near the base of interval 7 quite invisible from above ; the striae fine, with small concealed punctures ; the intervals even, each with a row of long erect blunt setae ; the scales convex, feebly fluted. *Legs* with dense light brown scaling, the hind femora with a paler band ; front tibiae not produced externally at the apex.

Length 3·0–3·5 mm., breadth 1·7–2·0 mm.

NATAL : York, 3 ♂, 5 ♀, xii.1938 (*G. Mackenzie*).

Reported by the Division of Entomology, Pretoria, as damaging young pine trees.

Allied to *L. setosus*, Boh., which has the eyes much less convex, the scape more gently curved, the elytra less broadly rounded behind, with the scales opaque, concave dorsally and with their hind margin elevated, and the setae sharply pointed.

Subfamily EREMNINAE.

Tanyremnus fallax, sp. n. (Plate XIII, fig. 4).

♂♀. Derm piceous brown, with rather uneven grey scaling, producing a mottled appearance ; underside with dense even grey scaling, often having a greenish reflection.

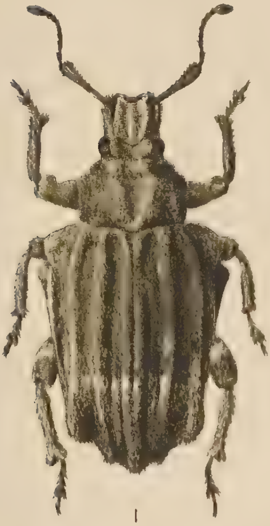
Head with very shallow confluent punctures, usually forming concentric curves on each side but normally hidden by scaling ; forehead very nearly as wide as the base of the rostrum, with a short median stria ; eyes only slightly more convex than the general curvature of the head. *Rostrum* a little longer than the pronotum, narrowing from the base to the middle then gradually widening again to the apex, the dorsal outline lower than that of the forehead, straight from the base to the antennae (inserted at two-thirds from the base), then sloping rather steeply to the apex ; the broad scrobes entirely visible from above, but becoming much shallower behind and not quite reaching the eyes ; the narrow raised median area transversely convex, minutely punctate, and with a very fine median carina on the basal half in ♀ but not in ♂. *Antennae* with the slender, abruptly clavate scape shortly exceeding the eye ; all the joints of the funicle much longer than broad, their order in diminishing length being : 1, 2, 3, (4, 5), 7, 6. *Prothorax* transverse (5 : 7), strongly rounded laterally, widest at the middle, feebly constricted at the apex, with the constriction continued across the dorsum, the base gently arcuate, the apical margin shallowly sinuate, the postocular lobes feeble ; the dorsum slightly convex longitudinally, very closely set with small flattened tubercles, without any median stria or carina, the scales usually forming a denser median stripe. *Elytra* very narrowly ovate in ♂ but rather broadly rounded at the apex, wider in ♀ and sharply acuminate at the apex, shallowly sinuate at the base, the basal angles very obtuse, with distinct rounded shoulders in ♀ (much less developed in ♂) and there broader than the widest part of the prothorax ; the striae rather broad and shallow, with small separated punctures ; the intervals broader than the striae, slightly convex, with a row of indistinct granules which are usually more evident posteriorly, each granule bearing a short subrecumbent curved spatulate seta. *Legs* red-brown, with rather sparse pale scales, forming an indefinite denser ring on the femora ; front tibiae of ♂ strongly curved inwards at the apex (much less so in ♀), the hind tibiae with the dorsal edge shallowly sinuate in both sexes.

CAPE PROVINCE : Krantzbosch, 2 ♂, 4 ♀, xi.1937.

Reported by the Division of Entomology, Pretoria, as damaging young plants of *Pinus taeda*.

Very similar to the only other known species of the genus, *T. loripes*, Boh., which is known to me only in the male sex and differs as follows:—Forehead distinctly narrower than the base of the rostrum and on the same level with it; elytra much more narrowed and compressed behind, being acuminate at the apex, with the suture somewhat elevated on the declivity, without any shoulders near the base and not wider there than the prothorax, the basal angles being almost rectangular; the front tibiae only slightly curved at the apex (even less than in the ♀ of *fallax*) and the hind pair straight dorsally.

T. loripes has previously been recorded (Bull. Ent. Res. **18,** 1928, p. 263) as damaging *Pinus pinaster*.



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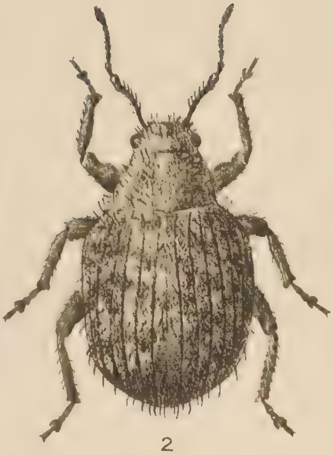

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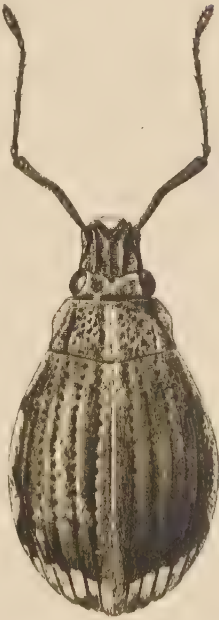

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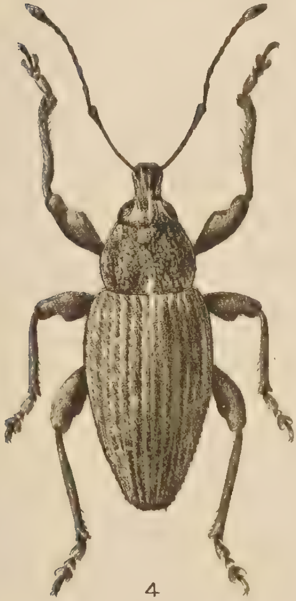

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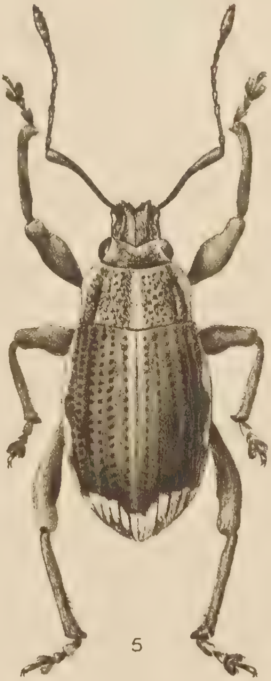

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O.F.T.

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1. *Glyptosomus angulatus*, Mshl., sp.n. ♀

2. *Lalagetes edax*, Mshl., sp.n. ♀

3. *Sciobius mordax*, Mshl., sp.n. ♀

4. *Tanyremnus fallax*, Mshl., sp.n. ♂

5. *Sciobius mordax*, Mshl., sp.n. ♂

AIR TRANSPORT, INSECTS AND DISEASE.

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Introduction.

In April 1935, the services dealing with scientific research in the Sudan underwent drastic reorganisation. A special sub-section of the newly-formed Agricultural Research Service was created to deal with all problems pertaining to medical entomology, and staff from the entomological section was detailed for duty with the research section of the Sudan Medical Service. The writer was appointed medical entomologist and placed in charge of this sub-section.

The discovery by Hewer (1934) of a possible case of yellow fever at Wau, and the presence in certain areas of the Anglo-Egyptian Sudan of large numbers of natives with immune bodies to yellow fever, had drawn attention to the danger of introduction of this disease by air, either by infected mosquitoes, or man, into the northern Sudan and Egypt, and thence perhaps into Europe and India. Immediate action had been taken by the medical authorities, and since the Wau case all aircraft entering the Sudan had been inspected and sprayed for insects.

With the creation, in 1935, of a medical entomological service, it was decided that a thorough investigation into the possibilities of the carriage of insects by aircraft should be undertaken. The work was started in July 1935.

It was realised that Khartoum airport afforded admirable facilities for this research for the following reasons :—

1. Khartoum was then (and has subsequently become more so) an important air junction, linking North, South, East and West African air lines.
2. Khartoum is a natural gateway from South, East and West Africa, leading to Egypt, Europe and India, and situated as it is, in the centre of the eastern Sahara, is the only route whereby pests and disease, carried by aircraft, can be transported from tropical Africa to Egypt, and the only point at which effective control measures can be taken.
3. Khartoum airports, both land and water, are so situated, the one on a stretch of the White Nile some distance from Khartoum itself, and the other on a sandy waste adjacent to the Royal Air Force landing ground to the east of Khartoum, that their invasion by insects is unlikely, particularly so in the case of mosquitoes. Khartoum itself is rigidly controlled by a highly efficient Sanitary Service, and it is rare to find an adult mosquito that has bred out within the city limits. The surrounding country is dry and arid, and except for the river fringe, not rich in insect life. The river for some distance north and south of Khartoum is constantly examined for pools formed by the receding floods, with the result that mosquito breeding within a 15-mile radius of Khartoum is kept extremely low. Mosquitoes that fly into Khartoum from the north during the winter are attracted to the green city, and are extremely unlikely to be found at either airport. The investigation into the insects carried by aircraft could, therefore, apart from the precautions natural to such research, be considered as being relatively little influenced by local fauna.

The work was finished in August 1938, and therefore comprises just over three years' research. The writer retired from the service of the Sudan Government in September 1938, and has since been working at the Imperial College of Science and Technology under Professor J. W. Munro.

At the beginning of the investigation it was intended merely to obtain information as to the number and kinds of insects found in aircraft alighting at Khartoum airport. With a review of the literature, however, and at the suggestion of Professor Munro, it was decided to extend the scope of the work.

Recent researches on yellow fever ; the transport of *Anopheles gambiae* from Africa to South America in 1930, and its subsequent spread and the consequences thereof ; the ever-growing network of the world's air communications (Map 3) ; and the increasing anxiety shown by many Governments, and by the League of Nations Health Organization, in connection with the carriage of insects by aircraft ; together with the results obtained during the work at Khartoum, have led the writer to attempt the more ambitious scope of the present paper.

Up till now the main danger arising to man with the increase of air transport has been the fact that epidemic and endemic areas of disease have been brought into close contact with the remainder of the world, and that natural barriers such as the oceans and the Sahara desert are no longer effective. It is perhaps natural that man's first reaction to the sinister implications of air transport should be in connection with the dangers of the spread of human disease. The potentialities for harm inherent in the vectors of animal and plant pathogenic organisms, and the transport of the pests of crops, are, however, fully as great, and should not be lost sight of.

Acting on the suggestions of Prof. Munro, a summary of the situation in regard to air transport, insects and disease, together with a consideration of the problems arising out of the control of insects in aircraft, are presented.

Malaria and Air Transport.*

Malaria is so widespread that it did not at first appear that the advent of aerial transport materially altered the *status quo*. The discovery by Shannon (1930) in March 1930, of the presence of *Anopheles gambiae*, a native of Africa, in the city of Natal, Rio Grande do Norte, Brazil, its subsequent spread, and the outbreaks of malaria resulting therefrom, have caused this view to be considerably modified.

A. gambiae was, until this discovery, known only in the Old World ; it was presumably carried, either by one of the fast French mail steamers, one of the French destroyers which were assisting in the survey of a transatlantic air line, or by one of the early transatlantic experimental flights. Up to 1930 aircraft had crossed the South Atlantic on eight occasions, most of them starting from Dakar or its vicinity and landing at Natal. Natal and Dakar and Bathurst are now the most important termini for Africa-South America air lines.

Shortly after the discovery of *A. gambiae* in Natal there occurred an unusually severe outbreak of malaria in the vicinity of its breeding-grounds. According to Davis (1931) by May the malaria situation had become serious. In 172 specimens caught in houses there was a malarial infection rate of 62·8 per cent., including 32 per cent. of salivary gland infections. According to the same author the indices are said to be without precedent in the literature on malaria.

Shannon (1932) stated that investigations carried out nine months after the first discovery, covering the coastal area of Brazil from Recife, Pernambuco, to Belem, Para, indicated that the species was still restricted to Natal ; this, however, was later proved not to be the case.

Fosdick (1939), President of the Rockefeller Foundation, in his " Review for 1938 " states : " in 1930 and 1931 there occurred in the vicinity of the breeding area in Natal an outbreak of malaria of a severity unprecedented in the annals of the city. The yellow fever service was compelled to undertake *gambiae* control in order to maintain an efficient staff for its own work. By 1931, following prevailing winds, *gambiae* mosquitoes had travelled up the coast 115 miles. Two years of severe dry seasons seemed to check the invasion, and then, with the recurrence of normal rainfall, the onward flight started again. In recent years severe epidemics of *gambiae*-carried malaria have occurred in localities over 200 miles west and north of Natal. In the Jaguaribe valley of the State of Ceara alone there were over 50,000 cases of malaria in 1938. Over 90 per cent. of the population was affected, with mortality in certain districts estimated at over 10 per cent. So disabling and widespread was the epidemic that, in some parts, crops were not planted and salt production was greatly reduced because of the lack of labor. It is estimated that as a result of the ravages of the mosquito nearly every person in these affected areas will be on Government relief in 1939."

According to Shannon (1932) " This is the first known case of a species of *Anopheles* pertaining to one faunal region being introduced into another."

Although *A. gambiae* is the major vector of malaria in a large part of Africa, the native population have built up a resistance to the indigenous malaria strain, and the possibility of epidemics such as that described by Fosdick is unlikely. It is considered that one reason for the remarkable results following upon the introduction of *A. gambiae* to South America is probably the fact that the native population appears to have little resistance to the African strain of malaria (according to de Souza Pinto (1931) exclusively *Plasmodium vivax*) carried by this mosquito. The same author (1938) states that in 397 mosquitoes he found 71·5 per cent. to have stomach infections with oöcysts, and 21·2 per cent. with salivary gland infections with sporozoites. In 1931–32, the mosquito, probably carried by the wind, spread up the Potengy and Ceara-Mirim Rivers ; in 1937–38 it spread up the Asson and Mossoro Rivers in the Rio Grande, and up the Jaguaribe River, in the State of Ceara. In Brazil the seriousness of the malaria epidemics caused by this mosquito is due to the mass of cases and the severity of some of them. Though the clinical symptoms are those of benign tertian, mortality is excessively high. This is ascribed to the high rate of infection in the mosquito, with consequent large numbers of re-infections in man. In some villages it is difficult to find one healthy inhabitant.

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* Bibliography—Section I.

The above short history illustrates the serious consequences which can follow the introduction of a vector from one malarial area to another. Little imagination is required to visualise the results of the introduction of malaria into a non-malarial territory suitable to the development of the disease.

Yellow Fever and Air Transport.*

The situation with regard to yellow fever is, potentially, far more serious than that of malaria. In 1930, quarantine regulations of airships against yellow fever were announced in America, and in India the Act of 1914 was amended to provide for precautions against the introduction of insects and other pests by air traffic. In 1931, Cook (Symposium on Malaria 1931) pointed out the danger of yellow fever being transported to Haiti by aeroplanes of the New York-South America service which called at Port au Prince. Hinman (1932) and Hindle (1933) have summarized the work on yellow fever up to their dates of publication, but the subject is so important in relation to air transport that the writer ventures to present a brief review of the biological and epidemiological aspects of the work done in recent years.

Insect and Tick Vectors of Yellow Fever.†

Until 1928 the control of yellow fever was in general considered to depend upon the control of *Aëdes aegypti*, although Manson had, in an early edition of the Handbook of Tropical Diseases (*circa* 1912–14) suggested that other Aëdine mosquitoes might act as vectors. In that year Stokes, Bauer & Hudson (1928), working in West Africa, proved that :—

> " 1. Yellow fever was successfully transmitted to *Macacus rhesus*.‡
>
> " 2. It was easily transmitted from man to monkey, as well as from monkey to monkey by the injection of citrated blood taken early in the course of the disease. It was also transmitted from monkey to monkey by *Aëdes aegypti*.
>
> " 3. Mosquitoes, when once infected, were found to remain infective for the entire period of their lives, which in our experience exceeded three months in some instances, and the bite of a single mosquito was sufficient to produce a fatal infection in a monkey.
>
> " 4. The virus was not transmitted from one generation of mosquitoes to another through the eggs . . . . "

And Bauer (1928) proved that *Aëdes luteocephalus*, *A. stokesi* (=*apicoannulatus*) and *Eretmopodites chrysogaster*, were able to transmit the disease by bite from monkey to monkey. These were outstanding discoveries, and paved the way for much important research.

1929 : Davis & Shannon (1929) proved that *Aëdes scapularis* could transmit yellow fever by bite, and that *Aëdes serratus* and *A. taeniorhynchus* retained the virus, and when ground up and inoculated produced fatal infections. Dinger et al. (1929), using 10 Rhesus monkeys, obtained one infection by bite with *Aëdes albopictus*. Monteiro (1929) induced clinical and post-mortem appearances of yellow fever by inoculating Rhesus monkeys with the faeces of *Cimex lectularius* which had previously been fed upon infected monkeys. Philip (1929) showed that *Aëdes vittatus*, *A. africanus* and *A. simpsoni* could transmit yellow fever by bite.

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* Bibliography—Section I.

† Only positive results are discussed here, and no reference is made to experimental work on *Aëdes aegypti* ; for fuller details see Trop. Dis. Bull. 1928 onwards.

‡ *Macacus rhesus* is now *Macaca mulatta*.

1930: Philip (1930) found that *Mansonia africana* (*Taeniorhynchus africanus*) could transmit yellow fever both by bite and by being inoculated into monkeys. *Anopheles gambiae* in similar experiments gave negative results after a period equivalent to that required for *A. aegypti*, but infection was produced by inoculation up to four days after the infecting feed. Philip (1930 *a*) also refers to unpublished lists in which *Aëdes irritans*, *A. nigricephalus*, and *Culex thalassius*, all gave positive results when inoculated.

1931: Davis & Shannon (1931) discovered that the virus survived for twelve or more days in *Aëdes terrens*, *A. serratus*, *Psorophora cingulata*, *P. ferox*, *Mansonia fasciolata*, *M. chrysonotum*, and *M. albicosta*. They also discovered (1931 *a*) that *Aëdes fluviatilis* was a carrier, obtaining 8 infections out of 11 trials, 3 of which were fatal by bite. *Aëdes taeniorhynchus* was found to be a less efficient carrier, only 1 in 10 producing a fatal infection by bite, although the virus remained alive in the bodies of the mosquitoes as proved by inoculation. Experiments with *Triatoma megista* were inconclusive.

1932: Kerr (1932) demonstrated that *Culex thalassius* was capable of transmitting the virus by bite, the mosquito remaining infective for 27 to 49 days after the infecting meal. *Mansonia uniformis*, although unable to transmit by bite, retained the virus for at least 24 days, possibly for its life. Kumm & Frobisher (1932) showed that although *Mansonia titillans* was incapable of infecting by bite, the virus remained alive, and monkeys inoculated with the contents of the mosquitoes at various intervals up to a maximum of 30 days after the infecting meal, became infected and died of yellow fever. In experiments with *Cimex lectularius* it was found that the virus died off so rapidly that the contents of the bugs failed to produce infection later than 2 days after the infecting meal.

1933: Aragão (1933) was successful in obtaining the transmission of yellow fever by bite of *Amblyomma cajennense*, *Ornithodorus rostratus*, and *O. moubata*; he also proved the infectivity of the eggs of *A. cajennense*. The disease was also induced by the inoculation of an emulsion made from female ticks; *A. cajennense* remained infective by inoculation for 14 days, but the *Ornithodorus* spp. could only retain the virus for 4 days. Davis (1933) induced yellow fever in *M. rhesus* by the injection of crushed adults of *Argas persicus*, *Amblyomma cajennense* and *Rhipicephalus sanguineus*, 6, 15 and 23 days after the infecting feed respectively, and of crushed nymphs of *R. sanguineus* and the larvae of *Boophilus annulatus microplus* 10 days, and of unidentified chicken mites 6 days after the infecting meal. After 28 days adults of *A. persicus* induced immunity without clinical indications of the disease. No evidence was obtained that the virus was passed from generation to generation via the egg, that it survived metamorphosis, or that it was transmitted by bite. Davis (1933 *a*) also proved in two experiments that *Culex fatigans* was able to transmit the disease by bite to *M. rhesus*; but in spite of these positive results the general evidence indicated that *C. fatigans* is not an efficient carrier, for in many cases the insects appeared to be able to free themselves of the virus. Davis (1933 *b*) in further experiments with *Triatoma megista* found that it was unable to transmit by bite, and the conclusion was reached that only by rare chance could this insect convey yellow fever.

1934: Hoskins (1934) showed that the dog flea, *Ctenocephalides canis*, when fed on *M. rhesus* infected with the Asibi strain of yellow fever, and then ground up in normal 10 per cent. serum and injected peritoneally into a healthy monkey 7 hours after the infected feed, produced yellow fever. The virus had disappeared from the bodies of the fleas 18 hours after the infecting meal. He also showed that *Stomoxys calcitrans* could transmit yellow fever by bite 6 hours after the infecting feed, but was not able to do so 16 hours after. Injections of *Stomoxys* gave positive results up to 42 hours after the infecting feed, but failed to do so at 48 hours after.

1937: Whitman & Antunes (1937) confirmed Davis* and Davis & Shannon's previous work on the efficiency of *Aëdes scapularis* and *A. fluviatilis* as vectors, and that *A. nubilis, A. terrens, Mansonia juxtomansonia, M. chrysonotum, M. fasciolata* and *M. albicosta*, retain the virus in their bodies. They also found that (Antunes & Whitman 1937) the Asibi strain of the virus was retained by *Haemagogus capricorni* (=*janthinomys*) for at least 2 weeks, although in only 1 case out of 6 were they successful in transmitting it by bite. They were unable to confirm the transmission of the virus by bite with *Aëdes taeniorhynchus* or *Psorophora ferox*. They suggest that there might be races of the latter possessing varying capacities for transmission. In a single experiment with *Haemagogus* sp. (probably *uriartei*) a strain of jungle yellow fever was used; it was retained in the body of the mosquito but not transmitted by bite. They suggest that incubation may perhaps be longer in this genus. Roubaud *et al.* (1937) showed that *Aëdes geniculatus*, a native of Europe which breeds in tree-holes and is a ready feeder on man and animals, was able to transmit the virus by bite 14 and 18 days after the infecting feed; 22 days after, suspensions of the mosquitoes were inoculated into 8 mice, which died of yellow fever after the usual interval.

1938: Whitman & Antunes (1938 *a*) demonstrated that the virus could be acquired by the larvae of *A. aegypti* when placed in a mixture of blood serum from an infected *M. rhesus* and an equal quantity of normal saline. When these larvae pupated 48 hours after, the pupae were transferred to tubes of clean water; adults began to emerge on the 4th day after contact with the virus, and the first 28 females were ground up and injected subcutaneously into a healthy monkey on the day of emergence. Four days later the monkey developed fever and the virus was found in its blood. In further experiments the larvae were transferred from the serum solution to clean water before pupation; a suspension of the resulting males was titrated in mice and the virus was found to be present. Larvae hatching from eggs which had been placed in the serum, removed on the day following hatching, washed and transferred to clean water, gave rise to 6 adults which were shown by titration in mice to retain the virus if the original infection was unusually large. Shannon, Whitman & Franca (1938) made an extremely important contribution to our knowledge of the vectors of the disease. During the 1938 outbreak of jungle yellow fever in the state of Rio de Janeiro they had mosquitoes collected from four points where human infection had occurred, and forwarded daily to the laboratory. Out of 24,304 wild mosquitoes received over a period of 11 weeks, yellow fever was produced in 2 monkeys by the bites of *Aëdes leucocelaenus* and *Haemagogus capricorni*. Furthermore, the intracerebral injection of an emulsion of 118 *H. capricorni* into mice produced typical yellow fever encephalitis; the same results were obtained from a similar experiment using 88 specimens of Sabethine mosquitoes. The following groups were tried:—*Aëdes fulvus, A. terrens, A. serratus, A. scapularis, A. leucocelaenus, Haemagogus capricorni, Psorophora ferox, P. albipes*; 3 spp. of Sabethines; all other Sabethines, totalling about 20 species.

These results are of the utmost importance, as they constitute the first positive evidence of a species in the natural transmission of jungle yellow fever in Brazil. Until this discovery the positive evidence as to the possibility of insects other than *Aëdes aegypti* being concerned in the transmission of yellow fever was furnished entirely by laboratory experiments. The fact that a given insect is able to transmit yellow fever virus in the laboratory does not necessarily mean that the same insect is either able or likely to do so in a wild state; it is an indication but not a proof. Concurrently with the laboratory research, however, a great deal of valuable work has been done in the field, and the suspicion had become conviction that insects other than *A. aegypti* were concerned in the transmission of yellow fever, particularly of jungle yellow fever. Shannon, Whitman & Franca have transformed conviction to certainty.

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* This paper includes unpublished results of the late N. C. Davis.

1939: Recently, Bennett, Baker & Sellards (1939) have transmitted yellow fever to *M. mullatta* with the North American *Aëdes triseriatus* under experimental conditions. They consider that this mosquito in its susceptibility to yellow fever occupies a position midway between *Aëdes aegypti* and altogether refractory species. The importance of this work is enhanced by the fact that *A. triseriatus* can exist under conditions which would be too severe for *A. aegypti*.

TABLE I.

Insects and Ticks proved to have transmitted Yellow Fever by Bite.

Insect	Distribution	Habits
Aëdes luteocephalus, Newst.	W. Africa, S. Sudan	Tree-holes, cut bamboos.
,, *stokesi*, Evans	W. Africa, Uganda	Tree-holes, banana stumps, cut bamboos.
,, *vittatus*, Bigot	Mediterranean region, Africa, India	Rock pools, drains, gutters, etc.
,, *africanus*, Theo.	Tropical Africa	Tree-holes, bamboo stumps, semi-domestic.
,, *simpsoni*, Theo.	,, ,,	Tree-holes, leaf axils, etc.
Eretmopodites chrysogaster, Graham	,, ,,	Tree-holes, banana stumps, tins, large fallen leaves.
Mansonia africana, Theo.	,, ,,	Larvae and pupae attached to roots of *Pistia*, and other aquatic plants.
Culex thalassius, Theo.	,, ,,	Coastal marshes.
Aëdes triseriatus, Say	N. America (outside endemic zones of Y.F.)	Tree-holes, small pools.
,, *scapularis*, Rond.	S. America	Ground pools, temporary rain pools, salt marshes.
,, *taeniorhynchus*, Wied.	Central and S. America	Rock holes, along stream beds.
,, *fluviatilis*, Lutz	S. America	Ground pools.
Haemagogus capricorni, Lutz	,, ,,	Tree-holes.
Aëdes albopictus, Skuse	Orient generally	Tree-holes and domestic.
Culex fatigans, Wied.	Tropics and sub-tropics	Domestic.
Aëdes geniculatus, Oliv.	Europe	Tree-holes.
Stomoxys calcitrans, L.	Cosmopolitan	Manure and debris.
Amblyomma cajennense, F.	Central and S. America	
Ornithodorus rostratus, Arag.	S. America	
,, *moubata*, Murr.	Africa	Domestic, native dwellings.
Aëdes leucocelaenus, Dyar and Shannon	S. America	Wild mosquitoes collected from points in jungle where human infection had occurred.
Haemagogus capricorni, Lutz	S. America	

N.B.—Riley & Johannsen include *Anopheles albitarsis* and *A. tarsimaculatus* as efficient experimental vectors (Riley & Johannsen, Medical Entomology, 2nd Ed. 1938, p. 252). The writer has been unable to verify these from the literature.

TABLE II.*

Insects, Ticks, etc., proved to retain the Virus of Yellow Fever and/or cause Yellow Fever when inoculated into Susceptible Animals.

Insect	Distribution	Habits
Aëdes irritans, Theo.	W. Africa	Brackish water.
,, *nigricephalus*, Theo.	,, ,,	Crab holes.
,, *punctocostalis*, Theo.	,, ,,	?
Mansonia uniformis, Theo.	Africa, India, Australia	Weedy swamps, *Pistia* plants.
Anopheles gambiae, Giles	Trop. Africa, Brazil†	Ground pools, river pools, etc.
Aëdes serratus, Theo.	S. America	Ground pools.
,, *terrens*, Walk.	,, ,,	Tree-holes.
,, *nubilis*, Theo.	,, ,, and W. Indies	Ground pools.
Psorophora cingulata, F.	C. and S. America	,, ,,
,, *ferox*, Humb.	,, ,, ,,	,, ,,
Mansonia titillans, Walk.	,, ,, ,,	Weedy swamps, *Pistia* plants, etc.
,, *juxtomansonia*, Theo.	,, ,, ,,	,, ,, ,, ,, ,,
,, *fasciolata*, Arrib.	,, ,, ,,	,, ,, ,, ,, ,,
,, *chrysonotum*, Pery.	,, ,, ,,	,, ,, ,, ,, ,,
,, *albicosta*, Lutz.	,, ,, ,,	,, ,, ,, ,, ,,
~~*Haemagogus capricorni*, Lutz.~~	~~S. America and Trinidad~~	~~Tree-holes.~~
Blatella germanica, L.	Cosmopolitan.	
Cimex lectularius, L.	Cosmopolitan in temperate zones	Domestic.
,, *hemipterus*, F.	Cosmopolitan in tropics	,,
Triatoma megista, Burm.	Brazil and Br. Guiana	,,
Ctenocephalides canis, Curt.	Europe and America	,,
Argas persicus, Oken	Cosmopolitan	Fowl and bird tick.
Rhipicephalus sanguineus, Latr.	Nearly cosmopolitan	Mainly on dogs, kennels.
Boophilus annulatus microplus, Can.	Australia, S. America, Africa, Asia	Cattle tick.
Chicken mites, unidentified	S. America.	
Hirudo medicinalis	Nearly cosmopolitan	The common leech.
Haemagogus capricorni, Lutz (an emulsion of 118)	S. America, Trinidad	Tree-holes.
88 specimens of Sabethines comprising about 20 species	,, ,,	Wild mosquitoes collected from points in jungle where human infection had occurred.

* If an insect has been proved to transmit yellow fever by bite as well as by inoculation it will be found only in Table I and will not be duplicated.

† This is not a native of Brazil, but was introduced from Africa in 1930 by mail steamer or aeroplane (see p. 367).

Jungle and Rural Yellow Fever.

The work done by doctors and entomologists on the epidemiology of the disease, and on the bionomics of the mosquitoes in epidemic and endemic areas, has completely altered our conception of the yellow fever problem. The difficulties of the control of the disease in endemic " silent " areas, and the danger of its spread by means of aircraft have been revealed by recent discoveries. In particular the " mouse protection test," whereby persons and animals showing an immunity to the disease can be ascertained, has enabled endemic " silent " areas to be delineated which would not otherwise have been classed as yellow fever areas at all.

The following brief review of work done since 1933 purports only to consider those papers which appear to the writer to have a bearing upon the problem of air transport. The vastly increased area of yellow fever country as revealed by the mouse protection test, viscerotomy, etc., the existence of jungle yellow fever without *A. aegypti* in South America, and of rural yellow fever with *A. aegypti*, and the strong indication that other insects play a part in the transmission of the disease, would seem, to the writer, to be of the greatest importance in any consideration of the problem of the control of insects in aircraft. Those wishing to study further the epidemiology of yellow fever, should consult the "Tropical Diseases Bulletin."

Soper *et al.* (1933) described an outbreak of yellow fever that occurred in 1932 in a rural district in Brazil, in which *A. aegypti* was not found, even after a thorough and prolonged search, which was begun six weeks before the apparently spontaneous disappearance of the disease. The most likely vector was considered to be *Aëdes scapularis*, but *A. fluviatilis* was also suspected. *Phlebotomus* spp. were the only other insects that could be considered. This was the first recorded case of jungle yellow fever (Pan. Afr. Hlth. Cong. 1935).

Hewer (1934) while engaged on a survey of yellow fever in the Anglo-Egyptian Sudan discovered a case at Wau, and gives the following summary :—" In summary, from the results of the mouse protection test it appears that yellow fever was present, probably in endemic form, in the Bahr el Ghazal six years ago; in Mongalla seven years ago ; in the Upper Nile Province between eleven and eighteen years ago ; in Darfur eighteen years ago ; and in the Nuba Mountains thirty years ago. There is no evidence that the disease was ever present in the desert areas to the North of the Sudan, the sera from El Obeid and Khartoum being entirely negative."

Soper (1935) states that cases have occurred in Brazil, Peru, Bolivia and probably Colombia, in localities where *A. aegypti* has not been found. Moreover, the disease exists in places where the population is so small and scattered as to suggest the presence of a vertebrate host other than man. It has also occurred at irregular intervals over a period of several years in areas where the population is relatively small, under conditions that suggest the existence of vectors of greater longevity than mosquitoes.

Soper (1935 *a*) pointed out that yellow fever is now known to exist in four forms, urban and rural in the presence of *Aëdes aegypti*, and rural and jungle without *A. aegypti*. The third form appears where the population of the rural areas is sufficient to suggest that the cycle of infection may be man-vector-man, but the fourth form occurs in rural and jungle areas and at isolated points along certain river banks where the human population is low, and its movements so small that the cases would seem to be accidents in an epizootic rather than part of an epidemic. Contrary to urban yellow fever, the greatest danger is where the human population is lowest and there is the most intimate contact with the jungle. *Haemagogus capricorni* is suggested as a likely vector.

At the Pan-African Health Conference held at Johannesburg (1935) it was revealed that the immunity survey of Africa, as analysed by Sawyer, showed that yellow fever was endemic in the following territories : French West Africa, Gambia, Portuguese Guinea, Sierra Leone, Liberia, Gold Coast, Nigeria, French Cameroons, Rio Muni, most of French Equatorial Africa, south-western Anglo-Egyptian Sudan, a portion of Uganda, the greater part of the Belgian Congo and northern Angola. The immunity survey of South America was similar to that of Africa in that it demonstrated that the endemic area was much greater than recent history of the disease had shown. From an immunity survey of the Amazon valley it was stated that the disease had continued endemic for many years in the " silent " Amazon regions of Brazil, Bolivia, Peru and Colombia ; that yellow fever had not remained endemic as the result of the dissemination of the virus from a few larger centres of population ; and that the disease had remained endemic in certain large districts of the Amazon valley in the absence of *A. aegypti*.

Sawyer & Whitman (1936) published the results of the mouse protection test on sera from Morocco, Algeria, Tunis, Egypt, Anglo-Egyptian Sudan, Abyssinia, British Somaliland, Madagascar, Bechuanaland, Union of South Africa, and Spanish Guinea, completing the investigation begun in 1931 and ending in 1935, on the geographical distribution of immunity from yellow fever in man in Africa. The following is largely taken from their summary :—Immunity is widely but irregularly distributed in a region extending from the coast of Senegal eastward for approximately 3,300 miles to the upper reaches of the White Nile in the Sudan. On the north this region is limited by the Sahara, on the west and south the boundary follows the coast of the Atlantic from Senegal to the extreme northern part of Angola and then runs east across Angola to the southern part of the Belgian Congo. The region as a whole may be considered endemic in the sense that the disease is always present and widely distributed. It may be divided into two parts, the one, western, which extends to the eastern border of Nigeria and includes the coastal regions from Nigeria to Angola, and the eastern region which is the remainder. The former is the home of epidemic yellow fever, the latter of endemic yellow fever, in which the disease has never been recognised, with one exception (Hewer 1934, Findlay & Davey 1936–1936 *a*).

Burke (1937) investigating an epidemic of jungle yellow fever occurring in the absence of *A. aegypti* in the Planalto region of the Matto Grosso in 1934–35, considered *Psorophora ferox, Haemagogus* sp. and *Aëdes scapularis* to be possible vectors. Lane (1937), as a result of outbreaks of jungle yellow fever at São Paulo towards the end of 1935, made mosquito surveys from December 1935 to June 1936. Fifty-four species of mosquitoes were found, *A. aegypti*, which had existed in towns and villages until control was started, was absent in the rural areas. *Psorophora ferox* and *Haemagogus capricorni* were considered to be the most likely vectors. In a second paper (1937) dealing with a survey of the Sorocabana region, where outbreaks of yellow fever had occurred chiefly among lumbermen, 46 mosquitoes were taken, the most numerous and widely spread being, in order of their importance, *Aëdes leucocelaenus, Haemagogus capricorni, Psorophora ferox, A. nubilis, A. serratus* and *Mansonia chrysonotum. A. aegypti* was not found.

Antunes (1937) worked in the municipalities of Restrepo and Villavicencio on the eastern slope of the Andes, during an outbreak of jungle yellow fever. The outbreak originated in or near the forests, for most of the patients had worked there, and very few women and children were infected without leaving the settlements, which were more or less distant from the forests. Some 60 mosquitoes and a number of other blood-sucking arthropods were taken in the forests. *A. aegypti* was absent. Infection may have been transmitted mechanically in the settlements by *Rhodnius prolixus*, Stål, which was common in the huts and attacked man, but it was considered that if this Triatomid, or *Ornithodorus venezuelensis*, Brumpt, or Simuliids, which were also common, were good vectors, the outbreak would have been much more serious. *Haemagogus capricorni*, which was the commonest mosquito, was considered to be the most likely vector.

Walcott *et al.* (1937) investigated an epidemic of yellow fever which originated from a case contracted in the jungle. The outbreak occurred during February–April 1936 in the town of Cambara, Parana, Brazil. The 25 urban cases all appeared in an area not more than 100 yds. in diameter in a part of the town infested with *A. aegypti*, in which resided a labourer who for three weeks prior to the outbreak of yellow fever had worked in the jungle about 10 miles from the town. The first urban case occurred 17 days after the onset of fever in the labourer. The epidemic subsided promptly after *A. aegypti* had been controlled.

Soper (1937) considers that the reported incidence of yellow fever in South America is not a safe index of its occurrence in endemic zones. Although visible outbreaks in urban and maritime localities may decline, or even cease for a time, there is a vast reserve of infection in the interior. Infection transmitted by *A. aegypti* has been much more widespread in the interior of north-eastern Brazil than was previously believed, and did not disappear spontaneously following the organisation of measures against *A. aegypti* in the principal centres of population.

The disease is endemic not only on the coast of north-eastern Brazil, but over the whole country except a few of the southern States, and also in Bolivia, Paraguay, Peru, Ecuador, Colombia and Venezuela, including many sparsely populated jungle districts where *A. aegypti* does not occur.

Kumm & Novis (1938) in a study of the mosquitoes of Marajo Island, Brazil, where cases of jungle yellow fever had occurred in 1934–35, found that the commonest biters of man by day in the forests were *Aëdes nubilis*, *Psorophora ferox*, and *Haemagogus capricorni*. No *A. aegypti* were found.

Finally Soper (1938) brings our knowledge of yellow fever in South America up to date in an admirable review of the present situation ; he states as follows :—" Studies since 1930 have shown that there were two unknown epidemiological factors which doomed to failure the attempt to rid the continent of yellow fever by sanitation of the endemic seed-beds of infection, viz. :—1. Rural yellow fever transmitted by *Aëdes aegypti*. 2. Jungle yellow fever occurring in the absence of *Aëdes aegypti*.* Epidemiologically these two types are quite distinct, and up to the present time have not been observed in the same geographical regions . . . . . *aegypti*-transmitted yellow fever is generally acquired indoors, tends to involve all non-immunes of all ages living in infected houses, and spreads from place to place along the routes of human travel. The disease is practically limited to man and is easily controlled by reduction of the density of the vector. Jungle yellow fever, on the other hand, is usually acquired in or at the edge of the forest during working hours by those whose occupation takes them to the woods, and does not tend, in the absence of *aegypti*, to involve other members of the household living under the same roof with infective cases. Exceptions to this rule generally indicate that the other members of the household also visit the jungle, or even that the house itself is in very intimate contact with the forest. The infection of man is apparently an accident occurring in the course of some cycle or cycles of infection in the jungle of which man is not an essential part. The infection apparently spreads throughout jungle areas without relation to routes of human travel."

He then refers to the capture of *Aëdes leucocelaenus*, *Haemagogus capricorni*, and a Sabethine, naturally infected in the woods (Shannon, Whitman & Franca, 1938) and states " and there is great deal of accumulated evidence, both scientific and hearsay, indicating that monkeys are infected in the jungle and that certain species, notably the howlers, die in large numbers at the time human infections are occurring in the forest." According to Soper the distribution of jungle yellow fever has now been extended to Panama and British and Dutch Guiana (Soper 1937–38).

With regard to Africa, Findlay, in the discussion following Soper's paper (1938) gives a brief but valuable review of the situation. He states :—" The endemic zone in Africa represents an area of just under 4,000,000 square miles. Stretching from the west coast it is bounded on the north by the Sahara, on the south by an irregular line passing across the northern part of the Belgian Congo, and on the east by the western part of Uganda and the Sudanese and Abyssinian frontier. Formerly it was believed that in the Anglo-Egyptian Sudan the White Nile represented the eastern limit. In the last few months, however, it has been possible to examine bloods from the Fung region between the White and Blue Niles . . . . from 10 to 50 per cent. of the sera examined show the presence of immune bodies to yellow fever. There is no reason why yellow fever should be limited by an international boundary and in all probability the endemic yellow fever area will be found to extend well into the foothills of the Abyssinian plateau. In the Nuba Mountains area to the west of the White Nile many of the villages show a high percentage of positives to yellow fever . . . . . among the evidence is that from a European medical officer whose serum was negative when examined in the spring of 1936. In the autumn of 1936, when in the Nuba Mountains, he suffered from an attack of fever and in January 1937 his blood protected and has continued to protect against yellow fever" (James, 1938). "Evidence is also forthcoming from the neighbourhood of Malakal that yellow fever has been present there during the last five years. In 50 bloods examined in the spring of this year, nine from persons under 16 years of age and 12 from persons over 16 were positive : the youngest donor was 5 years old.

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* Soper defines " Jungle Yellow Fever " as that form transmitted by mosquitoes other than *A. aegypti*, not necessarily in the absence of *A. aegypti* ; generally it amounts to the same thing, but not of necessity.

"In both Africa and South America from 20 to 25 per cent. of wild monkeys in endemic yellow fever areas show the presence of immune bodies in their sera. There is, however, one difference between African and South American monkeys, whereas in the New World some species, such as the red howler, are quite susceptible to yellow fever, no African species reacts to the virus with clinical symptoms except the Barbary ape, which, living in North Africa, is thereby sheltered from yellow fever by the barrier of the Sahara.

"The most striking difference between yellow fever in the Old and New Worlds is, however, that in the former it has not yet been possible to determine the existence of true jungle yellow fever, that is to say the transmission of the virus by mosquitoes other than *Aëdes aegypti*, since in Africa no rural area has yet been found from which this mosquito is absent. However, in many parts of Africa *A. aegypti* is to be found breeding both domestically and non-domestically. In the Nuba Mountains, for instance, the larvae of *A. aegypti* have been obtained from tree-holes, more especially in the baobab (*Adansonia digitata*) at distances from 2 to 3 miles from the nearest habitation."

In conclusion, recent aspects of the epidemiology of yellow fever may be admirably summarised by the following extract from a letter to the writer by Dr. G. M. Findlay, who has kindly permitted quotation :—

"If mosquitoes and vertebrates, especially man and monkeys, form the only links in the epidemiological chain of yellow fever, it is not easy to understand how the infection is maintained endemically in certain areas, especially in view of (1) the short life of the mosquito, (2) the absence of spread of the virus from the mosquito, either by contact or through the egg, and (3) the comparatively short time that the virus is present in the circulating blood of vertebrate hosts.

"It should be remembered that in addition to subcutaneous or intracutaneous injection by a biting insect, the virus can penetrate (1) the unbroken skin, (2) the mucosa of the alimentary tract of monkeys (Findlay & MacCallum 1939 & 1939 *a*). It is possible, therefore, that a non-vertebrate vector may be found either of longer life than the mosquito and/or able to transmit the virus hereditarily and such a non-vertebrate vector may not necessarily be a biting arthropod. Thus the virus will survive in the body cavity of *Blatella germanica* for 15 days after injection and in *Hirudo medicinalis* for 8 days after a meal on an infected monkey. These, of course, are only indications and it is not suggested that these species play any part in the epidemiology of yellow fever. However, monkeys have become spontaneously infected with yellow fever under laboratory conditions, in the complete absence of mosquitoes, and with evidence tending to suggest an arthropod vector which can live for some months."

Experimental Yellow Fever in Animals.

Experimental work has not been confined to the vector. Following upon the work of Stokes, Bauer & Hudson (1928) a great deal of research was carried out on the possibility of animals providing a reservoir for the virus. Hindle (1933) has summarised this work, and gives a table showing the species of animal, the result of inoculating with the virus, and the authority.

The writer has endeavoured to bring this summary up to date in so far as it may be of interest to entomologists and of significance with regard to aircraft. Work of a purely medical and experimental nature has not been included. The following table* is compiled from Hindle up to 1933 and from the literature from 1933 to date.

With regard to this table Dr. Findlay points out that all mammals so far tested after inoculation with the pantropic or ordinary strain of yellow fever allow the virus to circulate in the blood stream for a few days, and subsequently develop immune bodies. Only a few species when inoculated with this virus show clinical symptoms and pathological lesions similar to those exhibited by man. These species are (1) Asiatic monkeys, (2) the Barbary ape among African monkeys, (3) certain South American monkeys, (4) hedgehogs—thus limiting the list to Primates and Insectivora. The remainder usually only succumb if inoculated intracerebrally with the neurotropic strain.

TABLE III.

Experimental Animals infected with Yellow Fever.

Animal	Results of Inoculation	Authors
Chimpanzee, probably *Pan satyrus*	Resistant but blood develops anti-viral properties	Stokes, Bauer & Hudson, 1928. Pettitt & Aguessy, 1932.
Cercopithecus tantalus, Ogilby (Grass monkey)	Resistant but persistence of virus in blood	Bauer & Mahaffy, 1930.
Ditto	Susceptible	Lloyd & Mahaffy, 1936.
C. mona, Schreber (Mona monkey)	Resistant	Bauer & Mahaffy, 1930.
Ditto	Susceptible	Lloyd & Mahaffy, 1936.
Erythrocebus patas, Schreber (Hussar monkey)	Persistence of virus in blood with no obvious ill effects	Bauer & Mahaffy, 1930.
Ditto	Susceptible	Lloyd & Mahaffy, 1936.
Cercocebus torquatus, Kerr. (Collared monkey)	Persistence of virus in blood with no obvious ill effects	Bauer & Mahaffy, 1930.
Macaca mulatta, Zimm. (*Rhesus* monkey)	Susceptible	Stokes, Bauer & Hudson, 1928.
M. radiata, Geoffr. (Bonnet macaque)	,,	,, ,, ,, ,,
M. irus, Cuv. (Crab-eating macaque)	,,	Aragao, 1928, Lloyd & Mahaffy, 1936.
M. speciosa, Cuv. (Stump-tailed macaque)	,,	,, ,, ,, ,,
M. inuus, L. (Gibraltar ape)	,,	Pettitt & Stefanopoulo, 1930.
M. nemestrinus, L. (Pig-tailed macaque)	Slightly susceptible	Dinger, Schüffner, Snijders & Swellengrebel, 1930.
Papio sphinx, Geoffr. (Mandril)	Resistant but blood develops anti-viral properties	Pettitt & Stefanopoulo, 1929.
P. papio, Desm. (Guinea baboon)	1 of 3 died; protective anti-bodies in all three	Stefanopoulo & Nagano with Wasserman, 1937.
P. hamadryas, L. (Sacred baboon)	Resistant but blood develops anti-viral properties	Pettitt & Stefanopoulo, 1929.
P. jubilaeus, L.	Susceptible	van den Berghe, 1939 *a*.
Aotus trivirgatus, Humboldt (Night or Owl monkey)	Slightly susceptible	Davis, 1931.
Callicebus moloch, Hoffm.	,, ,,	,, ,,
Pithecia monacha, Humboldt (Saki monkey)	,, ,,	,, ,,
Saimiri sciurea, L. (Squirrel monkey)	Susceptible	Kuczynski, 1929; Lloyd & Penna, 1933.
Cebus macrocephalus, Spix (Capuchin monkey)	Slightly susceptible	Kuczynski, 1929.
C. variegatus, Geoffr. (Capuchin monkey)	,, ,,	Davis, 1930.
C. frontatus, Kuhl. (Capuchin monkey)	Susceptible	Lloyd & Penna, 1933.

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* Purely negative results are not included, except where there has been contradictory evidence.

TABLE III.—*Continued.*

Experimental Animals infected with Yellow Fever.

Animal	Results of Inoculation	Author
Lagothrix lagotricha, Humb. (Negro or Woolly monkey)	Slightly susceptible	Davis, 1930.
Ateles ater, Cuv. (Spider monkey)	Susceptible	,, ,,
A. paniscus, L. (Spider monkey)	,,	Lloyd & Penna, 1933.
A. variegatus, Wagn. (Spider monkey)	,,	,, ,, ,,
Alouatta senicula, L. (Howler monkey)	,,	Davis, 1930.
Hapale jacchus, L. (Common marmozet)	,,	Kumm, 1932.
H. albicollis, Spix (Marmozet)	Susceptible, but disease unlike human	Davis, 1930.
,, ,, ,,	Susceptible	Lloyd & Penna, 1933.
Midas ursulas, Geoffr. (Tamarin)	Susceptible, but disease unlike human	Davis, 1930.
Dog	Survival of virus in blood for a few days	Monteiro, 1930.
Dog (puppies)	Clinically resistant, but P.M. suggestive of Y.F.	Nicolau & Baffet, 1937.
Cat	Survival of virus in blood for at least 30 days	Monteiro, 1930.
Cat	Negative results	Nicolau & Baffet, 1937.
Cat (kittens)	Susceptible	da Fonseca & Artegas, 1938.
Nasua narica, L. (Coatimundi)	Dies paralysed when inoculated intracerebrally	,, ,, ,, ,,
Tayra barbara, L. (Weasel family)	Susceptible	,, ,, ,, ,,
Cavia porcellus, L. (Guineapig)	Modified infection	Dinger, Schüffner & Snijders, 1930.
,, ,, ,,	Susceptible	Stefanopoulo & Wasserman, 1933.
,, ,, ,,	,,	Theiler, 1933.
,, ,, ,,	,,	Findlay, 1933.
,, ,, ,,	Susceptible to ordinary as well as mouse neurotropic virus	Mathis, 1934.
C. aperia, Margrave (Guinea-pig)	Susceptible	da Fonseca & Artegas, 1938.
Hydrochoerus capybara, Erzleben (Capybara)	,,	,, ,, ,, ,,
Ctenomys spp. (Toucotoucos)	,,	da Fonseca, 1938.
Mus musculus, L. (House mouse)	,,	Laigret, 1933.
M. musculus gentilis, Brants. (African race)	,,	,, ,,
,, ,, ,, ,,	Refractory to viscerotropic, susceptible to neurotropic	Mathis, 1936.
M. musculus azoricus, Schinz.	Susceptible	Laigret, 1933.
M. musculus spretus, Lataste	Refractory to viscerotropic, susceptible to neurotropic	Mathis, 1936.
Sciurus vulgaris, L. (Red squirrel)	Susceptible	Findlay, 1934.
Microtus agrestis, L. (Field vole)	,,	,, ,,
Citellus citellus, L. (Ground squirrel)	Barely susceptible	Stefanopoulo & Nagano, with Wasserman, 1937.
Erinaceus europaeus, L. (Common hedge-hog)	Susceptible	Findlay & Clarke, 1934.
Atelerix albiventris, Wagner (Sudan hedgehog)	,,	Findlay, Hewer & Clarke, 1935.
A. albiventris (probably), Nigeria	Resistant	Findlay & Mahaffy, 1936.

TABLE III—*Continued.*

Experimental Animals infected with Yellow Fever.

Animal	Results of Inoculation	Author
A. albiventris (probably), Nigeria	Susceptible	Smith, 1936.
Sus scrofa, L. (Pig)	,, ...	Stefanopoulo, Mollaret & Desnos, 1934.
Tayassu tajacu, L. (Peccary)	,, ...	da Fonseca & Artigas, 1938.
Cabassous unicinctus, L. (Armadillo)	No symptoms, but possible isolate virus after 5 days	,, ,, ,, ,,
Dasypus novemcinctus, L. (Armadillo)	Paralysed on 5th and 9th day, impossible isolate virus	,, ,, ,, ,,
Didelphyidae (American Opossums)	Slightly susceptible ...	,, ,, ,, ,,
Didelphys aurita	Virus isolable from brain ...	,, ,, ,, ,,

TABLE IV.

*Results of Mouse Protection Tests in Animals.**

Country and Animal	No. of Sera Examined	No. Protecting	No. not Protecting
ANGLO-EGYPTIAN SUDAN			
Galago senegalensis, Geoffr. (Bushbaby) ...	3	0	3
Erythrocebus patas, Schreber (Patas monkey) ...	1	0	1
Cercopithecus aethiops centralis, Neumann (Grass monkey)	15	1	14
SIERRA LEONE			
Colobus vellerosus, Geoffr. (Guereza monkey) ...	1	1	0
LIBERIA			
Cercopithecus spp.	10	4	6
GOLD COAST			
Cercopithecus spp.	1	0	1
C. diana diana, L. (Diana monkey)	1	1	0
Erythrocebus patas, Schreb.	1	0	1
Colobus vellerosus, Geoffr.	5	3	2
Procolobus badius badius, Kerr. (Red guereza) ...	6	3	3
P. badius waldroni, Hayman	3	1	2
Colobus spp.†	1	1	0
UGANDA			
Cercopithecus aethiops centralis, Neumann ...	20	5	15
BELGIAN CONGO			
Colobus polykomos, Illiger‡	11	1	10
FRENCH GUINEA			
Chimpanzee†	1	1	—
Baboon†	1	1	—

* This table is from Findlay & MacCallum (1937) with the exception of those items marked thus†, which are from Findlay, Stefanopoulo, Davey & Mahaffy (1936), and marked thus‡ which is from van den Berghe (1939).

Findlay states that the results on sera of Herbivora, cattle and sheep show that certain members of these species are capable of neutralising the yellow fever virus in the mouse protection test ; *e.g.*, positive cattle from England, India, Tanganyika and Kenya (James, 1937).

Conclusions on the Relation of Air Transport to Malaria and Yellow Fever.

Epidemiology of Malaria.

The salient fact that arises from the study of the literature is the danger resulting from the introduction of a malarial vector from one geographical area to another; firstly because of the possibility that the population of the area into which the vector has been introduced may prove to be remarkably susceptible to a plasmodium or strain of plasmodium new to that area, and secondly because the habits of the introduced mosquito may be such as to call for radical and costly alterations in anti-mosquito measures.

Covell (1927 & 1931) gives lists of 33 species of mosquitoes which are vectors, or suspected vectors on epidemiological grounds, of malaria throughout the world. Others have been added since. Weyer (1939) brings the subject up to date ; breeding-places, habits and relation to malaria of 46 species, including the principal vectors, are given.

Epidemiology of Yellow Fever.

The aspect of most importance with regard to aerial transport arising out of recent work on the epidemiology of yellow fever would seem to be the existence of vast areas in Africa and South America in which the disease exists either in epidemic or endemic forms (Maps 1 & 2). The distribution of endemic yellow fever in both these continents is very much greater than was thought, even so recently as a year ago, and the extent of these areas is increasing. It is of vital importance that Governments and air line companies concerned should keep up to date on this point.

Insect Vectors of Yellow Fever.

The work of the last ten years has produced a list of some 17 insects and 3 ticks capable of transmitting yellow fever by bite, and of some 21 insects, 3 ticks, a mite and a leech, able to retain the virus in their bodies for periods varying from a few hours to many days. These results, although achieved under laboratory conditions, have been corroborated by many investigations of jungle yellow fever in the field, and the recent work of Shannon, Whitman & Franca (1938), in presenting the first direct evidence of the transmission of yellow fever, under natural conditions, by mosquitoes other than *A. aegypti*, has lent added significance to the list of experimental vectors.

Equal in importance is the discovery by Findlay & MacCallum (1939 & 1939 *a*) of the possibility of infecting monkeys with yellow fever *via* the alimentary canal. This achievement must focus attention upon the list of those insects able to retain the virus in their bodies, but unable to transmit it by bite. The following facts, while not in themselves forming a complete chain of evidence, are nevertheless of considerable interest, and at least suggestive of possibilities.

1. Certain monkeys and hedgehogs are susceptible to the pantropic strain of yellow fever.
2. Most monkeys are partly,* and hedgehogs entirely, insectivorous. In both cases a wide range of insects is devoured.
3. The cockroach, *Blatella germanica*, L., has been proved to retain the virus within its body cavity for 15 days.
4. Monkeys have become spontaneously infected with yellow fever under laboratory conditions and in the complete absence of *Aëdes aegypti*.
5. *Blatella germanica* was present in the laboratory when the above-mentioned " spontaneous " infections occurred.
6. *Blatella germanica* and other cockroaches have, on several occasions, been found in aircraft.

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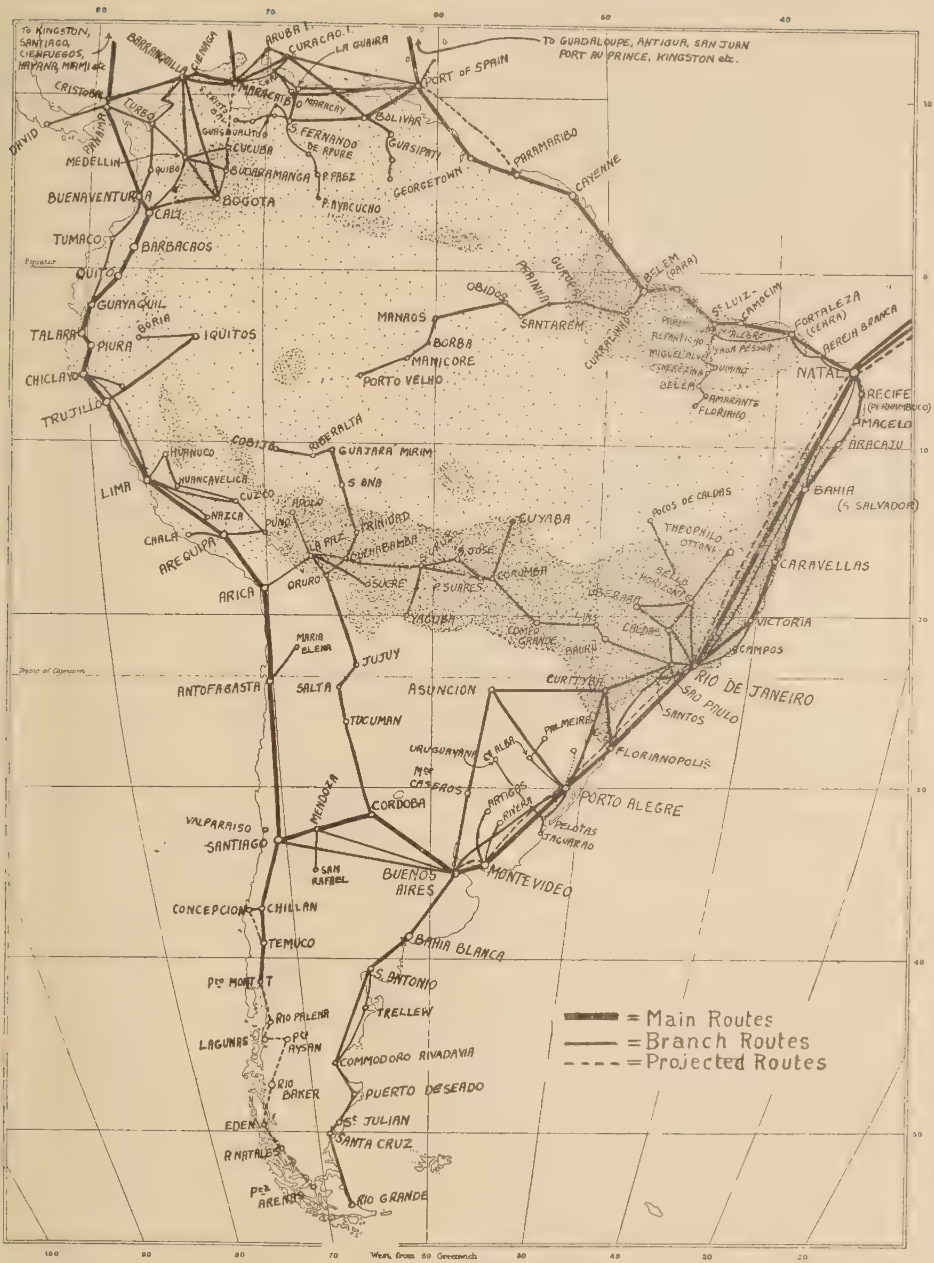
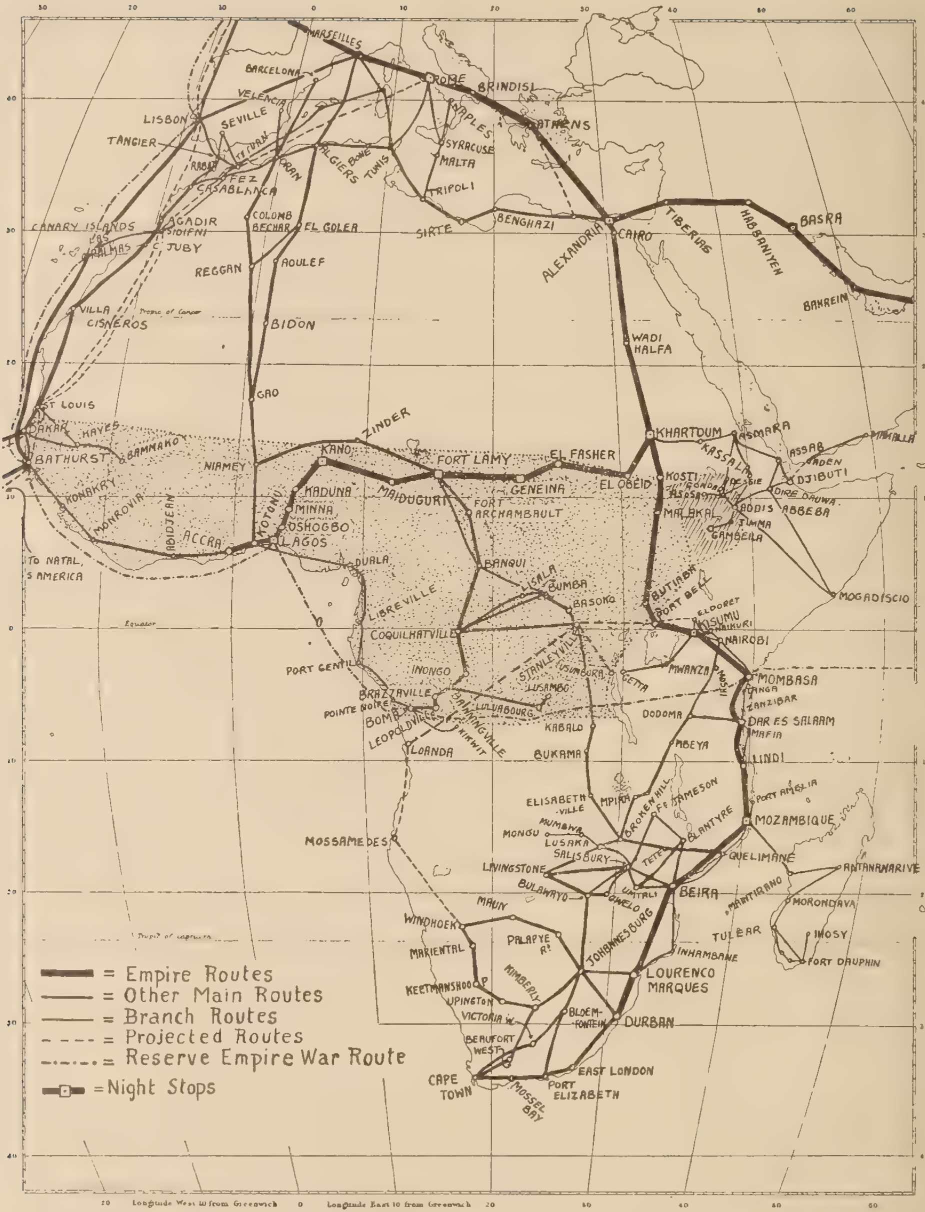
* Mr. R. I. Pocock of the British Museum (Natural History) informs the writer that in his experience nearly all monkeys are largely insectivorous and will eat any insect they can catch. The insect portion of their diet is probably greater than is usually imagined.


To KINGSTON, SANTIAGO, CIENFUEGOS, HAVANA, MIAMI etc.
TO GUADALOUPE, ANTIGUA, SAN JUAN PORT AU PRINCE, KINGSTON etc.
BARRANQUILLA
CIENAGA
ARUBA I.
CURACAO I.
LA GUAIRA
PORT OF SPAIN
CRISTOBAL
DAVID
PANAMA
TURBO
MARACAIBO
MARACAY
BOLIVAR
GUASIPATY
S. FERNANDO DE APURE
CUCUBA
BUCARAMANGA
P. PAEZ
MEDELLIN
QUIBDO
BUENAVENTURA
BOGOTA
CALI
P. AYACUCHO
GEORGETOWN
PARAMARIBO
CAYENNE
TUMACO
BARBACAOS
Equator
QUITO
GUAYAQUIL
TALARA
PIURA
BORJA
IQUITOS
MANAOS
OBIDOS
SANTAREM
BELEM (PARA)
S^t LUIZ
CAMOCIM
FORTALEZA (CEARA)
AREIA BRANCA
NATAL
RECIFE (PERNAMBUCO)
MACEIO
ARACAJU
BORBA
MANICORE
PORTO VELHO
CHICLAYO
TRUJILLO
COBIJA
RIBERALTA
GUAJARA MIRIM
HUANUCO
HUANCAVELICA
LIMA
CUZCO
S. ANA
NAZCA
PUNO
TRINIDAD
CUYABA
CHALA
AREQUIPA
LA PAZ
COCHABAMBA
S. JOSE
CORUMBA
ARICA
ORURO
SUCRE
P. SUARES
YACUIBA
BAHIA (S. SALVADOR)
CARAVELLAS
VICTORIA
CAMPOS
RIO DE JANEIRO
SAO PAULO
SANTOS
MARIA ELENA
JUJUY
ANTOFAGASTA
SALTA
ASUNCION
CURITYBA
Tropic of Capricorn
TUCUMAN
PALMEIRA
URUGUAYANA
FLORIANOPOLIS
CASEROS
CORDOBA
MENDOZA
ARTIGAS
RIVERA
PORTO ALEGRE
PELOTAS
JAGUARAO
VALPARAISO
SANTIAGO
SAN RAFAEL
BUENOS AIRES
MONTEVIDEO
CONCEPCION
CHILLAN
TEMUCO
BAHIA BLANCA
P^to MONTT
S. ANTONIO
RIO PALENA
TRELLEW
LAGUNAS
P^to AYSAN
COMMODORO RIVADAVIA
RIO BAKER
PUERTO DESEADO
EDEN
S^t JULIAN
SANTA CRUZ
P. NATALES
P^ta ARENAS
RIO GRANDE
= Main Routes
= Branch Routes
- - - - = Projected Routes
West from 60 Greenwich

Map 1. South America.—Rough map showing the main air routes and approximate areas of yellow fever. Heavy stippling indicates the approximate areas of yellow fever based on Soper (1937 and 1938) and Pan. Afr. Hlth. Conf. (1935), etc. Light stippling indicates the probable area in which there might be potential danger to aircraft from infected insects.


= Empire Routes
= Other Main Routes
= Branch Routes
= Projected Routes
= Reserve Empire War Route
= Night Stops
MARSEILLES
BARCELONA
ROME
BRINDISI
NAPLES
ATHENS
VELENCIA
LISBON
SEVILLE
TANGIER
RABAT
FEZ
CASABLANCA
ORAN
ALGIERS
BONE
TUNIS
SYRACUSE
MALTA
TRIPOLI
CANARY ISLANDS
LAS PALMAS
AGADIR
SIDIFNI
C. JUBY
COLOMB BECHAR
EL GOLEA
REGGAN
AOULEF
SIRTE
BENGHAZI
ALEXANDRIA
CAIRO
TIBERIAS
HABBANIYEH
BASRA
BAHREIN
VILLA CISNEROS
Tropic of Cancer
BIDON
WADI HALFA
GAO
ST LOUIS
DAKAR
HAYES
BATHURST
BAMMAKO
NIAMEY
ZINDER
KANO
FORT LAMY
EL FASHER
KHARTOUM
ASMARA
ASSAB
ADEN
MAKALLA
DJIBUTI
KASSALA
EL OBEID
GENEINA
KOSTI
MAIDUGURI
KADUNA
MINNA
OSHOGBO
KOTONU
LAGOS
ACCRA
ABIDJEAN
MONROVIA
KONAKRY
FORT ARCHAMBAULT
MALAKAL
GOBA
ADDIS ABEBA
DIRE DAWA
JIMMA
GAMBEILA
TO NATAL, S AMERICA
DUALA
BANQUI
LISALA
BUMBA
BASOKO
JUBA
BUTIABA
PORT BELL
KISUMU
ELDORET
NAKURI
NAIROBI
MOGADISCIO
Equator
LIBREVILLE
COQUILHATVILLE
PORT GENTIL
INONGO
STANLEYVILLE
USUMBURA
GETTA
MWANZA
MOSHI
MOMBASA
TANGA
ZANZIBAR
DAR ES SALAAM
MAFIA
BRAZZAVILLE
POINTE NOIRE
BOMA
LEOPOLDVILLE
BANNINGVILLE
KIKWIT
LUSAMBO
LULUABOURG
KABALO
DODOMA
MBEYA
LOANDA
BUKAMA
LINDI
ELISABETHVILLE
MPIKA
BROKEN HILL
FT JAMESON
PORT AMELIA
MOZAMBIQUE
MONGU
MUMBWA
LUSAKA
SALISBURY
TETE
BLANTYRE
QUELIMANE
MOSSAMEDES
LIVINGSTONE
BULAWAYO
UMTALI
GWELO
BEIRA
MANTIRANO
ANTANANARIVE
MORONDAVA
MAUN
WINDHOEK
PALAPYE R.
JOHANNESBURG
TULEAR
IHOSY
FORT DAUPHIN
INHAMBANE
Tropic of Capricorn
MARIENTAL
KIMBERLEY
LOURENCO MARQUES
KEETMANSHOOP
UPINGTON
VICTORIA W.
BLOEMFONTEIN
DURBAN
BEAUFORT WEST
EAST LONDON
CAPE TOWN
MOSSEL BAY
PORT ELIZABETH
Longitude West 10 from Greenwich
Longitude East 10 from Greenwich
30
20
10
0
10
20
30
40
50
60

Map 2. Africa.—Rough map showing the main air routes and approximate area of yellow fever. The stippling indicates the probable area of recent endemic yellow fever based on Sawyer's protection test data (Soper—Rep. Pan. Afr. Hlth. Conf. 1935, and Findlay in Soper, 1938). The area of cross-hatching indicates the probable extension of the area to the Abyssinian foothills (Findlay in Soper, 1938). Note the reserve Empire war route.

N.B.—The western "epidemic" area is not shown as such, but is of course included in the endemic area. For details see pp. 374 and 375.

These are indications rather than evidence, but cockroaches are omnivorous, and no considerable employment of imagination is necessary to see a possible connection between dead mosquitoes, excreta from other sick monkeys, and general detritus, etc., infected with the virus; scavenging cockroaches, and monkeys catching the cockroaches. The possibilities of such a cycle of infection are not confined to the laboratory, and it is reasonable to suppose that infection *via* the alimentary canal may possibly be a contributory cause of jungle or rural yellow fever; the ability of the flea *Ctenocephalides canis* to retain the virus may be of significance in this respect. The transmission of the virus by the bite of *Aëdes geniculatus* in Europe, and *A. triseriatus* in North America, although achieved in the laboratory, nevertheless indicates the possibility, should the virus be introduced, of the disease becoming epidemic in parts of the world that are too cold for the other known or potential vectors. A study of the list of insects found in aircraft (Table X) lends still further significance to the work done on insect vectors of yellow fever.

Susceptible Animals.

The list of animals which have been tested for their susceptibility to yellow fever would appear to indicate that, up to the present, only Primates and Insectivora are susceptible to the ordinary or pantropic strain of the virus. Relatively very few animals have, however, been experimented upon, and with the continuation of this line of work, together with further investigations into the immunity of wild animals by means of the mouse protection test, a vast reservoir of susceptible animals of many species may be revealed. Sinton (1934) has pointed out the potential danger with regard to monkeys in India, and the facts that a wild animal like the Sudan hedgehog is susceptible to the ordinary strain of the virus, is insectivorous, and that the virus can, in the case of monkeys, be introduced *via* the alimentary canal, are of the greatest importance when the foregoing data are considered together with the wide range of insects collected from aircraft (Table X).

From the point of view of air transport the general conclusion to be drawn would seem to be incontrovertible. Aircraft operating within and from Africa and South America should be maintained free from all insects. The proposed reserve Empire war route across Africa to India and Australia will present an urgent problem in this connection. It would be unwise to begin such a service before the control of insects in aircraft has been achieved.

Other Insect-borne Diseases and Insect Pests.

Although the mosquito-borne diseases, malaria and yellow fever, are the most important from the point of view of the spread of disease by means of aircraft, it should not be forgotten that there are many others, both virus and organismal, which are carried by insects, and which might at any time assume considerable importance if introduced to new territories. Findlay (1936 & 1939) has listed the insect-borne virus diseases of man and animals, and discusses the latest implications of research on viruses. Du Toit (1933) discusses diseases of animals that might be transported by aircraft. Among the insect-borne diseases he mentions East Coast fever (*Theileria parva*), anaplasmosis and Nairobi sickness (a virus). Ticks are the major vectors, and, as he points out, an infected tick may live for a year or more without food. Moreover it is not only in the spread of major endemic diseases from geographical area to geographical area that the danger lies. Onchocerciasis might easily be introduced from Central Africa to Khartoum or similar areas by the transportation of infected *Simulium*, and if this should occur during the *Simulium* season much harm might result. Modern text-books and the literature of Medical Entomology furnish many such examples, and from a medical point of view alone it would seem imperative that aircraft in the tropics generally should be kept entirely insect-free.

Little work has been done upon the carriage by aircraft of agricultural pests, and as yet no major pest has, as far as the writer is aware, been transported alive by an aeroplane from an infested country to a free area. The wide range of insects collected from aircraft, together with the discovery of the remains of a dead specimen of *Leucopholis irrorata*, Chevr. (Pemberton, 1938), the cane root grub pest of the Philippines, in an air clipper from the Orient suggest that such an occurrence is not only possible, but, in the opinion of some workers, probable, unless vigorous steps are taken to prevent it. From the agricultural as well as the medical aspect, the control of all insects in aircraft is imperative.

Air Lines of the World.*

From the preceding sections of this paper the importance of the ever-expanding network of air communications with regard to insect-borne disease will be evident. At the present time there are approximately 195 air line and charter companies operating throughout the world, the regular services of which cover a total of over 300,000 miles. They are distributed as follows :—Great Britain 32, Europe 33, Africa 14, Asia 17, North America 40, Central and South America 36, Australasia 23. Map 3 shows the world routes, while Maps 1 and 2 illustrate in more detail the air lines of South America and Africa, and the areas of potential danger to aircraft from yellow fever.

The information does not pretend to be completely accurate, as air routes are continually expanding and changing. It will, however, emphasise the importance of the control of insects in aircraft in these continents.

The Flight-Range of Insects and the Control of Airports.

Insects and Wind.†

In considering the question of the spread of disease by means of aircraft from the aspect of the insect vector, the problem resolves itself into the prevention of insects entering aircraft. There are two means whereby insects might be able to enter an aeroplane : (1) When it is stationary on the ground or on the water ; and (2) when the aeroplane is in flight.

In the first case there are two methods of control : (*a*) By making the aerodrome as insect-proof as possible, and (*b*) by destroying the insects once they have entered the aeroplane so that they shall not be introduced to the next landing-place. If the first method were possible to 100 per cent. degree of efficiency the last would become unnecessary. The first method is, however, unfortunately far from being a practical proposition, and in the tropics, at any rate, the cost of rendering an airport entirely insect-proof would involve so much clearing and screening that it would be prohibitive. Furthermore it is evident from a study of the literature on the flight-range of insects and their dissemination by wind, that even the most ambitious scheme might on occasion be useless.

It is apparent from the available evidence that the control of insects in aircraft cannot be narrowed down to one or two species of mosquitoes ; from a general medical and economic point of view all animals other than man, or properly quarantined animals belonging to passengers, must be prevented from entering and being transported by aircraft. In certain areas it is advisable that passengers should be able to furnish clean medical history sheets with regard to yellow fever.

Col. F. P. Mackie, medical adviser to Imperial Airways, has recently issued a brief note and map of Africa in connection with air traffic and yellow fever, in which he interprets in non-legal language, the terms "authorised," "sanitary," and "anti-amaryl" as applied to aerodromes, as follows:—

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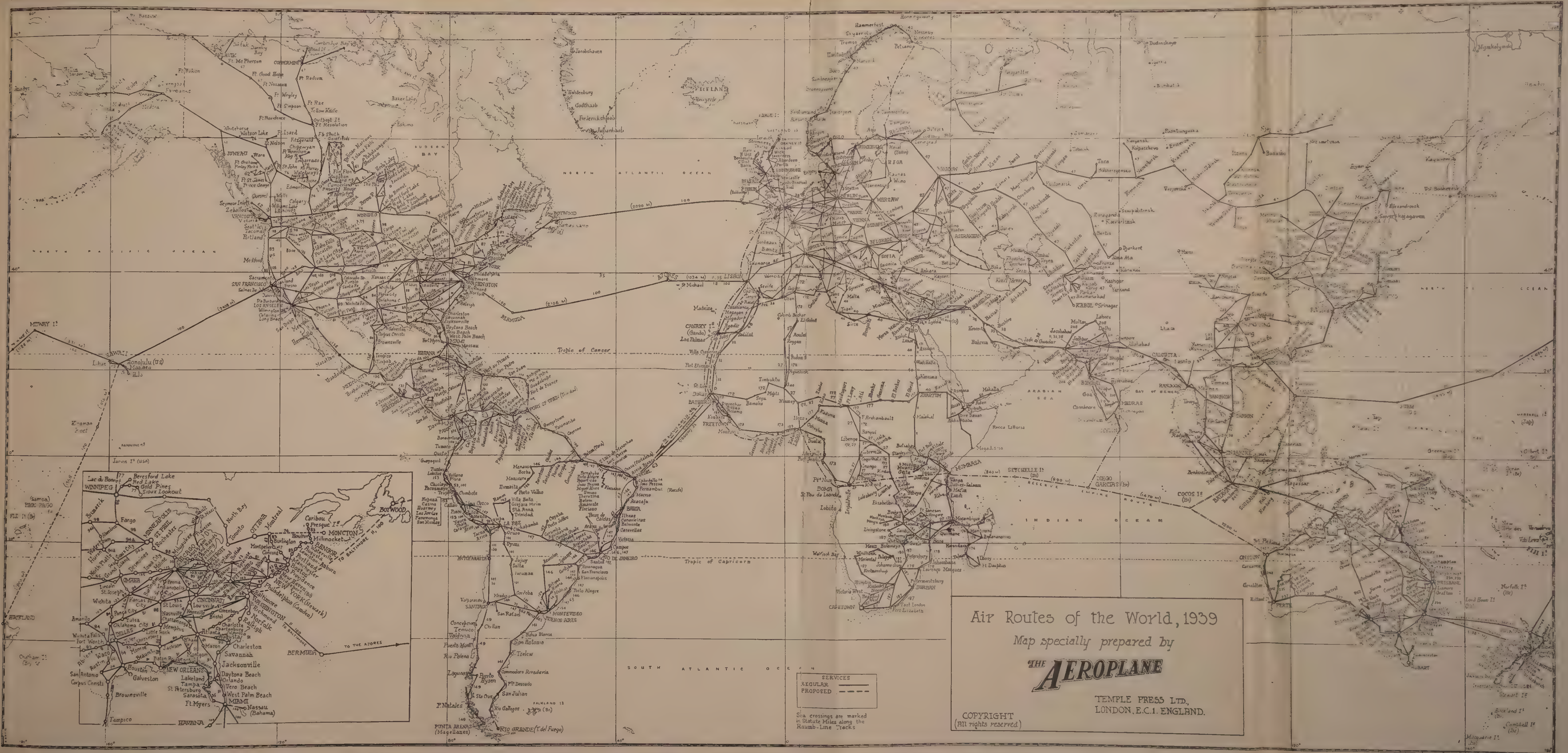
* This information was accurate up to the outbreak of war.

† Bibliography—Section 3.



Air Routes of the World, 1939

Map specially prepared by

THE AEROPLANE

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SERVICES
REGULAR
PROPOSED
Sea crossings are marked in Statute Miles along the Rhumb-Line Tracks
NORTH ATLANTIC OCEAN
NORTH PACIFIC OCEAN
SOUTH ATLANTIC OCEAN
INDIAN OCEAN
Tropic of Cancer
Tropic of Capricorn
HUDSON BAY
ARABIAN SEA
BAY OF BENGAL
TO THE AZORES
TO BALTIMORE
BERMUDA
AZORES
LISBON
HONOLULU (U.S.)
MIDWAY I.
CAPETOWN
DURBAN

John Bale Sons & Curnow Ltd London

"An *authorised* aerodrome is a customs area in which an aircraft can alight on its first entry into a particular territory, or from which it can depart when leaving that territory.

"A *sanitary* aerodrome is an authorised aerodrome which in addition is provided with certain medical facilities. It must have a medical officer and sanitary inspectors, a place for medical inspection, means for taking specimens for laboratory investigation, facilities for isolating suspected persons and equipment for disinfecting aircraft and its contents.

"An *anti-amaryl* aerodrome has the constitution and equipment of the authorised and sanitary aerodrome, but in addition has special provisions to guard against yellow fever. It must be situated at a safe distance from human habitation, its water-supply guarded against mosquito breeding, provision must be made of mosquito-proof buildings for the use of the crews and staff of the aviation service, and lastly, it must be provided with mosquito-proof accommodation for all passengers, both for their protection and for the isolation of any suspected case among them."

It would seem at first sight that an anti-amaryl aerodrome goes a long way towards achieving the ideal in insect proofing. This is to a certain extent true, but only in so far as the buildings are concerned, for it will be made clear later in this paper that a very considerable area of country would have to be cleared before an aerodrome in its entirety could be deemed safe from insect invasion. Taylor (1934) states that at Gadau, Northern Nigeria, tree-hole mosquitoes, including *Aëdes aegypti*, *A. luteocephalus*, and *A. simpsoni*, are able to exist under the most adverse conditions. The greater part of the annual rainfall, which averages only 25 inches, occurs during the period mid-June to mid-September and during the dry season the humidity is extremely low. No rainwater remained in certain observed tree-holes for longer than a few hours at a time until the beginning of July. In January and February after the grass fires, which often scorch the tops of the trees, were over, collections of debris and scrapings were taken from the holes and placed in water so that eggs present might hatch. Four species of *Aëdes* were reared, including *A. aegypti* and *A. simpsoni*. In order to complete this aspect of the control the aircraft also would need to be efficiently protected, either by insect-proof hangars, and in many aerodromes in the more remote parts of the world hangars do not exist at all, or by some means whereby the aircraft themselves, although out in the open, could be rendered insect-proof.

In view of the many different opinions that have been expressed on the matter and its obvious importance in relation to the control of insects in aerodromes, it will be as well to consider from every aspect the flight-range of insects.

The term "flight-range" may be misleading unless it is precisely defined. From an academic point of view the flight-range of an insect should mean the distance that a given insect is able to, and normally does, travel in the ordinary course of its life-history. This may, according to species, mean deliberate flight with or against the wind, or flight only on calm days. Research may determine the normal flight of a species, but it will not take into account the accidental dispersal of that species due to abnormal climatic conditions, nor must the deliberate flight-range of an insect be confused with the distance that the same insect may, on occasion, travel owing to wind drift.

As early as 1902 (Webster) and probably before that, the part played by wind, particularly in the form of storms, in the dissemination of insects had been recognised. Tower (1906) describes how the Colorado potato beetle (*Leptinotarsa decemlineata*, Say) spread from the Rockies to the Atlantic coast in about 15 years owing to wind dispersal during the autumn. Bonnet (1911) studied the fauna of the air ; Webster & Phillips (1912) discuss at length the influence of wind on the diffusion of *Toxoptera graminum*, Rond., the Aphids having been observed flying with the wind.

Stabler (1913) proved that in the spread of red spiders by wind a distance of 105 feet could be covered. Shtcherbakov (1914)* noted that very young larvae of *Lymantria dispar*, L., possessed very long thin hairs or aerophores, by means of which they were dispersed by the wind. Collins (1915) confirmed Shtcherbakov. Quale (1916) found that the young black scale *Saissetia oleae*, Bern., were carried by the wind, distances of 450 feet having been recorded. Collins (1917) working on the dispersion by wind of the gypsy moth (*Lymantria dispar*) found that distances of 19 to 20 miles had been covered. McColloch (1917) experimenting with wind-screens found that hessian flies (*Mayetiola destructor*, Say) were dispersed by wind, being on occasion carried over hills to uninfested valleys beyond. Nuttall (1917) states that lice (*Pediculus humanus*, L.) can be carried by light winds for a distance of several metres.

Hurd (1920) considers that two of the most sharply defined extensions of the cotton boll weevil (*Anthonomus grandis*, Boh.) in Texas occurred in 1915 and 1916 and were largely due to the sweeping winds in those years. He quotes other instances such as the buffalo gnat (*Simulium*) of Memphis brought by wind across the Mississippi, and according to this author Washington was a malarial city until the Potomac flats were drained, as the night winds used to bring the mosquitoes into the city. Börner (1923) records long distance flights of Aphids, observed at Memmert and Heligoland, of 15 miles at least. Folsom (1923) states that the buffalo gnat emerging from its breeding waters may be carried by winds to appear suddenly in enormous numbers 20 miles or more away, and that according to Trimen moths and longicorn beetles have been found 230 miles west of the African coast, and *Sphinx convolvulus*, L., has been recorded as flying aboard ship 420 miles from land. Elton (1925) found *Syrphus ribesii*, L., the spruce Aphid (*Dilachnus piceae*, Pz.) and a Tipulid on the surface of the snow at North-East Land (Spitzbergen) which can only have come from the Kola Peninsula, 800 miles across the sea, as that is the nearest land with spruce. Felt (1925), in a brief summary of the data on this subject, cites the cotton moth (*Alabama argillacea*, Hbn.), the corn ear worm (*Heliothis obsoleta*, F.), and a number of other southern moths, as probably drifting on the prevailing southerly and south-westerly winds. He states that the monarch butterfly (*Anosia plexippus*, L.) has spread widely in the Pacific Ocean within the last half of the preceding century, presumably taking advantage of favourable winds. Felt (1926), discussing the occurrence of insects outside the regions in which it is possible for them to become established owing to climatic conditions, argues that such occurrences may be attributed to the agency of air currents. He cites the following :—The Mexican Dexiid, *Cholomyia inaequipes*, Bigot, in the Pacific States, *Tabanus septentrionalis*, Loew, in New York and New England, and many others. The same author (1926 *a*) quotes the instance of Krakatoa and states that in August 1883 the entire group of islands was covered from 90 to 180 feet deep by molten larva, yet when they were visited 20 years later 64 species of insects were found ; 80 per cent. of the animals of these islands are winged. Caffrey & Worthley (1927) maintain that the European corn borer (*Pyrausta nubilalis*, Hb.) is dispersed by winds and that marked specimens were recovered which must have drifted across Cape Cod Bay, a distance of 20 miles. Loos (1927) records that the nun moth (*Lymantria monacha*, L.) travels in swarms with the wind, the flight itself being about 6·5 m.p.h. These moths can cross mountains over 3,300 feet in height. Bristowe (1929) describes how spiders, by means of gossamer, can travel for many miles, quoting instances ; thus the Arctic island of Jan Mayen, 300 miles from land, entirely of volcanic origin and never joined to any land mass, had 5 species of spiders living on it. Similarly St. Paul's Rocks, 540 miles from the coast of South America, with a highest point of only 50 feet above sea-level, of volcanic origin and rising steeply from the ocean bed, were stated by Darwin to harbour numerous spiders.

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* In 1893 Wachte & Kornanth described the aerostatic setae of the 1st stage larvae of *Lymantria dispar*, L., and *L. monacha*, L., and suggested that they assisted in the dissemination of the young larvae by wind.

Marcovitch & Stanley (1930) consider the phenomenal spread of the Mexican flea-beetle (*Epilachna corrupta*, Muls.) in the eastern United States to be due to the prevailing wind. Uvarov (1931) discusses the subject at length and gives many instances not included here. Roney (1932) has shown that the turnip aphis (*Rhopalosiphum pseudobrassicae*, Davis) is dispersed by wind. Smith & Allen (1932), discussing the migratory habits of the spotted cucumber beetle (*Diabrotica duodecimpunctata*, F.), state that a distance of 500 miles or more may be covered during 2–4 days in good weather, and aeroplane records show that altitudes up to 1,000 feet or more may be attained by the flight. Ehrlich (1933) states that the disease of beech caused by *Nectria coccinea*, following attack by *Cryptococcus fagi*, Bär., is spread because both fungus and insect are disseminated by wind. Collins & Baker (1934) state that records indicate that during a 40-year period *Porthetria dispar*, L., spread 2 to 2½ times as rapidly to N.E. and S.E. as towards N.W. and S.W. owing to prevailing westerly winds. MacDonald & Loftin (1935) came to the conclusion that all the indirect evidence indicates that the pink boll-worm (*Platyedra gossypiella*, Saund.) flies with or is carried by winds for considerable distances. Dorst & Davies (1937) found that the beet leaf-hopper (*Eutettix tenellus*, Baker) travelled 200 miles in about two days when moving from its breeding areas to the beet-growing area. Dispersal is stated to be influenced by wind and temperature. Felt (1937, 1937 *a*) considers that the spread of Dutch elm disease, carried by the elm bark beetle (*Scolytus multistriatus*, Marsh.) is due to the dispersal of this insect by wind. He gives many other instances of comparatively heavy insects being carried by winds. Ivanov & Zhitkevitch (1937) maintain that *Loxostege sticticalis*, L., when flying with the wind can sometimes travel 95 miles. Kirichenko (1937) considers that the spread of the San José scale in Russia is caused mainly by wind. Tucker (1937) states that the newly hatched larvae of *Diatraea saccharalis*, F., are drifted from some distance on air currents. Clarke (1938) found in New Zealand that the Coccid *Eriococcus coriaceus*, Mack., is distributed by wind ; it first appeared in 1900 at Timaru on the east coast of the South Island, and reached the North Island, carried by wind, in 1921. Gaines & Ewing (1938) consider that the cotton flea-hopper (*Psallus seriatus*, Reut.) in its transference from its native food-plants to cotton may, assisted by wind, travel considerable distances, the dispersal being at least 20 miles. Hardy (Hardy & Milne 1938) quotes passages from his diary while on board the R.S.S. " Discovery " in 1925, recording that " on the 26th October 1925 (16° 23′ 20″ N., 18° 27′ 15″ W., 130 miles from the African coast) : More insects have come aboard to-day than ever before : several butterflies, numbers of moths and beetles and countless grasshoppers, locusts and flying bugs. The latter were a perfect pest, appearing everywhere." And again on 13th October, 310 miles from Portugal and 340 miles from Morocco, he recorded " Spurge hawk moth or allied species, Silver ' Y ' moth, other moths and a red admiral butterfly," and on 15th October, 295 miles from the African coast, " a death's head hawk moth was taken on board."

Finally, Dr. J. A. Freeman has very kindly lent the author his unpublished typescript of " Studies in the Distribution of Insects by Aerial Currents " (see also Freeman, 1938) and has permitted quotation. It is a valuable contribution to the subject, and should, when published, be consulted by those interested. The conclusions from his work are discussed under " The Insect Population of the Air."

The foregoing is, of course, far from being a complete survey of the dispersal of insects by wind. Sufficient has nevertheless been quoted to show (*a*) the considerable distances that insects of widely differing types are able to cover by the aid of wind, (*b*) the number of insects of economic importance whose dispersal has been aided by wind, and (*c*) the difficulty of maintaining aerodromes free from insects. It may be pointed out that many insects are able to traverse enormous distances without the agency of mechanical means of transport, and that therefore the danger of aircraft is exaggerated. It should be remembered, however, that what nature may do in periods of time varying from one year to half a century or more, the aeroplane may do in a few hours. Moreover, in spite of prevailing winds there are certain natural barriers such as the Sahara and the oceans that appear to be effective in maintaining the various geographical regions separate from one another, and these areas of adverse climatic conditions are sufficiently great to destroy most wind-borne flying insects. The aeroplane removes these barriers, and provides a means of travel for insects, combining speed with shelter, that no other form of communication is able to do.

*The Flight-Range of Mosquitoes.**

The literature on the flight-range of insects is widely scattered, and much of it is buried in papers upon other subjects and does not therefore appear under its own subject heading in the libraries and bibliographies; a certain amount of work has, however, been done on mosquitoes, a brief summary of which is given here. There are probably many valuable records of which the writer is unaware, and any information on this subject would be of very great interest and would be gratefully received.

Engeland (1913) considered that if a ship were anchored less than a mile from the shore, and particularly if a land wind were blowing, Anophelines might be found on board in large numbers. Wright (1918) records that swarms of *Anopheles pulcherrimus*, Theo., appeared on a hospital ship when lying off the Shat el Arab 15½ miles from the nearest land; not a single mosquito had been noticed on the voyage from Bombay, and a search revealed no breeding-place on board. À Court (1918) describes an outbreak of malaria that occurred on board a hospital ship at Sierra Leone. The ship arrived during the height of the malaria season and anchored 2,000 yards from the shore. During the evening of the 3rd day a fresh anchorage was taken up 1,130 yards from the shore. An off-shore breeze sprang up and many mosquitoes were noticed on board at nightfall. A malarial outbreak followed. Of the 690 persons on board 35 contracted malaria, of whom only one had landed, and that by daytime. Kligler (1924) considers that under constant wind conditions the distance of spread of Anophelines from their breeding-places appears to vary directly with the intensity of breeding and inversely with the density of settlements in the neighbourhood of the breeding-places. The standard distance for routine control should not be less than 1½ miles. He considers that the prevailing wind is also of importance. Low (1925), in the course of anti-malarial work at Ismailia, records that during strong winds *Anopheles pharoensis*, Theo., was always prevalent in the camp, the invasion arising from marshes about 5 miles distant. Swellengrebel (1925) states that the flight-range of *Anopheles maculipennis*, Mg., must, from the evidence of adults in houses away from breeding-places, be increased from 500 to 1,000 metres. The same author (1929), during the course of anti-mosquito measures within a 2-mile radius from the centre of Medemblik in the Zuider Zee, discovered that prevailing winds would carry the mosquitoes away from their feeding-grounds. In a certain locality the daily catch was 3 times as great when the winds had passed over an untreated breeding-place, as on days of a sea wind. Kligler (1931) working on the long-range dispersal of *Anopheles* found that " during the pre-hibernating and hibernating periods *Anopheles elutus*, Edw., are found in villages 14 kilometres from the nearest breeding-place." Symes (1931) states that *Anopheles gambiae*, Giles, has a flight-range of over 3 miles. De Meillon (1937) carried out operations on the flight-range of *A. gambiae*, in Northern Rhodesia, and found that flying with the wind these mosquitoes can fly 2 miles in a single night, and in a slight breeze they do not fly close to the ground and so are not hindered by dense bush of an average height of 20–30 feet. Afridi & Majid (1938), in experiments with marked *Culex fatigans*, Wied., in the Delhi urban area found that a distance of 3 miles was within the power of this mosquito.

The writer, while engaged in research on mosquito-eating fish, found that a pool in Khartoum, heavily stocked with the fish *Gambusia affinis*, Baird & Girard, inspected daily and cleared of all eggs, larvae and pupae twice a week, was continually re-infested by egg-laying mosquitoes, both *Culex* and *Anopheles*. It is impossible that these mosquitoes could come from the Khartoum area, which is effectively controlled by the Sanitary Service, while the country surrounding Khartoum is inspected and kept clear of mosquito breeding for a radius of over 10 miles. The re-infestation of the pool continued for over two months, thus rendering unlikely the suggestion that the egg-laying arose from a few individuals which were hanging about the pool. It was considered that the mosquitoes probably originated from the river cultivation north of Khartoum and travelled for at least 10 miles, assisted by the prevailing north wind.

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* Bibliography—Section 2.

With regard to the genus *Aëdes*, Cooling (1924) states that *A. vigilax*, Skuse, is said to have an average ordinary range of 3 miles under favourable conditions, but there is evidence that in Queensland this species will travel ordinarily from 5 to 10 miles and probably 20 or even 40 miles. Stage, Gjullin & Gates (1937) found that the flood water mosquitoes, *Aëdes vexans*, Meig., and *A. aldrichi*, Dyar & Knab, in the lower Columbia River valley could fly, both with and against general wind currents, for at least 2 miles, and greater distances (3 and 5 miles) were recorded. Cuming (1931) records that *Aëdes aegypti* is said to fly from 400 to 1,000 metres. Shannon & Davis (1930) in experiments in the flight-range of *A. aegypti* came to the conclusion that a flight of more than 300 metres is not exceptional among the *Stegomyia* of a representative community, and that a sustained flight over water of one kilometre is well within the range of possibility. Hinman (1932) states that the adults of *A. aegypti* are incapable of more than a few hundred yards flight. Soper (Rep. Pan. Afric. Hlth. Conf. 1935) considers that *A. aegypti* might fly long distances in exceptional circumstances, but the studies of adult densities permit the localisation of foci of breeding to within, generally, 25 yards. Findlay (Soper, 1938) records how in the Nuba Mountains *A. aegypti* has been obtained from tree-holes at distances of 2 to 3 miles from the nearest habitation. The locality in question is well known to the writer and it is his opinion that *A. aegypti* may, in certain circumstances, fly a mile or more, but much work requires to be done before any definite opinion on the flight-range of this mosquito can be expressed.

The information on the flight-range of mosquitoes is meagre and disjointed, yet the sum total of evidence inclines to the belief that, even in the case of *A. aegypti*, a notoriously urban and shelter-loving species, its capacity for travel is probably greater than is generally thought and allowed for in all circumstances. With regard to the Anophelines the available evidence points to a considerable range of action. This conclusion taken into consideration together with the widened list of known and suspected vectors of yellow fever, the number of Anophelines known to be capable of transmitting malaria, and the various other diseases capable of being transmitted by mosquitoes, adds additional weight to the importance of preventing all species of CULICIDAE from being carried in aircraft.

The Insect Population of the Air.*

It has been stated that there are two means whereby insects may gain access to aircraft : when the aircraft are stationary, and when they are in flight. The last possibility has never been thoroughly investigated, and although such evidence as exists would seem to indicate the unlikelihood of such entry, nevertheless a definite pronouncement upon the question would be premature without some further research, particularly in view of recent work on the insect population of the upper air. Of recent years much valuable work has been done upon the fauna and flora of the atmosphere, and the writer has collected the essential data upon the subject.

Work upon the insect population of the atmosphere may be divided into two sections, that dealing with the "terrestrial" zone of the atmosphere, *i.e.* up to about 150–200 feet, and that dealing with the upper air, which may be described as being from 200 feet upwards. It is not, of course, possible to divide the literature exactly into these two sections, as some papers deal with altitudes ranging from 10 feet to 2,000 feet. It is, however, practical to differentiate work which relied only upon the height of existing edifices and did not utilise mechanical means of gaining altitude, such as kites or aircraft, from that which did employ these means.

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* Bibliography—Section 3.

The Terrestrial Zone of the Atmosphere.

Weiss (1927 & 1928) investigated insects taken at forest look-out stations in New Jersey. The towers varied in height from 40 feet to 200 feet, and all of them were above the tops of the trees. Their elevations above sea-level were for the most part well in excess of the tower heights. Rice (1933) operated flight-traps in the vicinity of Moscow, Idaho, of which the height varied from 6 inches to 65 feet, and the elevations of the sites were from 2,750 feet to 4,050 feet. Riggert (1931) made studies of the vertical distribution of frit flies up to a height of 60 feet, using sticky screens. Felt & Chamberlain (1935) collected insects found on the roofs of the following tall buildings : The State Education Building at Albany, N.Y., some 128–148 feet above the street level ; a building of 30 stories in the centre of New York ; another of 11 stories at Mount Vernon ; the 35 foot fire tower at Crane Mountain at an altitude of 3,254 ft. ; and the 60 foot fire tower at Hill 7, Stephentown, at an altitude of 1,960 ft. Approximately 1,000 species of insects were captured ; among the most interesting were 6 species of gall wasps, although the nearest oaks were approximately one mile away ; the Colorado potato beetle (*Leptinotarsa decemlineata*, Say), which is a heavyish insect ; the plantain leaf-miner (*Dibolia borealis*, Cher.) which feeds upon low-growing plants ; the clover leaf weevils, *Hypera punctata*, F., and *H. meles*, F. ; the pales weevil (*Hylobius pales*, Boh.), although pines were over a mile away ; bill bugs (*Calendra zeae*, Walsh), though an expert consulted had no idea they could fly ; a leaf-hopper, *Acucephalus albifrons*, L., with such distinctly subterranean habits that special collecting is ordinarily necessary ; the recently introduced Japanese Scarabaeid *Aserica castanea*, Arrow, which is a somewhat heavy insect ; and many others. The authors conclude from these records that a much more general movement of insects at some height in the air occurs than is generally supposed. Table V indicates the orders of insects, together with the number of families and species collected by Weiss (1927 & 1928)*, Rice (1933) and Felt & Chamberlain (1935).

Reference to the original papers will reveal that many of these are heavy insects and strong fliers, and it is of interest to compare the number of orders and families with the results obtained from collecting in the upper air (Table IX).

*The Upper Air.**

Stakman *et al.* (1923) were the first to use aircraft in the study of aerial population. They found spores, fungi, small insects, pollen grains and glumes of grass up to 11,000 ft. Spores were found at 16,000 ft.

Coad (1931)† used an aeroplane and specially designed traps, insects below 50 ft. were not considered. He found that the densest population was within the first 1,000 ft. ; at 2,000 ft. there were approximately half as many as at 1,000 ft., and at 3,000 ft. half as many as at 2,000 ft.

From 3,000 ft. to 5,000 ft. there was comparatively little difference, while from 6,000 ft. upwards the population was considerably lighter. Computations were made of the numbers of insects in a column of air one mile square starting 50 ft. from the ground and extending 14,000 ft. up. Computing from several hundred collections which had been made it was shown that under all conditions for all seasons of the year in the vicinity of Tallulah, La., an approximate average of 25,000,000 insects was to be found in the upper air over this square mile of ground. The lowest ebb was in January when the figure dropped to about 12,000,000, and the highest was during May when it reached 36,000,000. As a rule the larger, stronger flying insects were found closer to the earth (3,000 ft. or lower) and the smaller, weaker ones at the higher altitudes. The minute parasitic flies and wasps, the plant lice and mites, were found up to 14,000 ft.

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* For details of orders and families and the altitudes at which they were caught see the composite table at the end of the section (Table IX).

† Coad gives no details of his catches.

TABLE V.

Height Range of approximately 6 *ft. to* 250–300 *ft.*

Order	Weiss		Rice		Felt & Chamberlain	
	No. of Families	No. of Species	No. of Families	No. of Species	No. of Families	No. of Species
Diptera	26	53+*	11	30	41	194
Hymenoptera	13	39+	21	115	14	47
Lepidoptera	13	31+	7	32	19	78
Coleoptera	22	45+	39	211	43	477
Orthoptera	3	4+	3	8	3	7
Homoptera	4	12+	6	33	8	63
Hemiptera	7	7+	14	56	11	73
Odonata	3	6+	—	—	—	—
Ephemeroptera... ...	1	1+	1	5	1	3
Plecoptera	2	1+	—	—	1	1
Trichoptera	1	2+	1	1	4	6
Neuroptera	4	3+	3	4	4	5
Megaloptera	1	1	—	—	—	—
Isoptera	—	—	1	1	1	1
Corrodentia	—	—	1	1	2	6
Arachnida	Argiopoidea				Araneidae	
	Ixodidae				4	8
Totals ... 14	100	205	108	497	156	969

* The number of families have been taken from both Weiss's papers, but the number of species from his 1927 paper only. The results of the two papers are similar and the + signs after the figures indicate the few additional species not mentioned.

Lienhart (1931) in the course of assisting in the landing of many balloons was struck with the rich harvest of animal and vegetable matter found in the baskets. Owing to the slow movements of the balloons the insects were in excellent condition. He gives the following list, unfortunately making no mention of the height at which they were found (in view of other worker's results it is probable that these particular insects entered the baskets at low altitudes, either while the balloons were ascending or descending) :—Ephemeroptera of the genus *Chloe*, Libellulidae (*Calopteryx splendens*, Harris, and *Agrion elegans*, Vanderlind), *Chrysopa chrysopa*, L., *Phryganea varia*, F., *Pieris brassicae*, L., *P. napi*, L., *Vanessa cardui*, L., *V. atalanta*, L., *V. io*, L., *Stenobothrus*, *Tipula*, *Tabanus*, Hymenoptera of the genus *Chrysis*, *Coccinella 7-punctata*, L., and *Adalia bipunctata*, L. He makes the interesting statement that although he has examined many aeroplanes on landing he has never seen a single organic element adhering to them.

Smith & Allen (1932) record that aeroplanes have encountered the spotted cucumber beetle (*Diabrotica duodecimpunctata*, F.) at altitudes of 1,000 ft. or more during the migratory flights of this insect, and quote a Mr. Stanley to the effect that he has seen the beetle moving southwards at altitudes of 4,000 ft. to 6,000 ft.

Macdonald & Loftin (1935) took pink boll-worm moths (*Platyedra gossypiella*, Saund.) up to 3,000 ft.

Felt (1937) mentions that several bark-beetles have been taken in aeroplane traps in Lousiana at 200, 500 and 2,000 ft.

Berland (1933–34–35–36–37) carried out extensive research on the fauna of the upper air, using aircraft and special collecting nets. He considers that the atmosphere may be divided into two layers, a lower one which he terms the " terrestrial " zone, extending from 1 metre to 20 metres above the earth, and containing by far the greater majority of insects, including all strong-flying or heavily built species, and an upper one which he calls the " plankton " zone, extending from 20 metres to 5,000 metres (16,404 ft.), in which the insects are much smaller and lighter, usually not exceeding 2·3 mm., and with very weak powers of flight, the most frequent being small flies. The plankton zone contains, as well as small insects, plant debris, spikelets of grain, ears of corn, bits of leaves, and even mineral particles of about 1 mm. in diameter. Berland originally considered (1935) that the terrestrial zone extended up to 200–300 metres, but in subsequent papers (1936–37) he reduced this estimate to 20 metres, stating that large insects are only found up to about this height. The reason for this is that the plankton zone is populated by means of vertical currents and the more powerful and heavier insects are able to resist these and keep nearer the soil. Felt (1926 *b*) also mentions such currents, stating that there are convectional air currents at 1,200 to 4,500 ft. with recorded velocities of 2,000 ft. per minute.

Collins & Baker (1934), exploring the upper air for wind-borne gypsy moth larvae (*Porthetria dispar*, L.), found four first instar larvae during two seasons' flight, one at 300–500 ft., two at 1,000 ft. and one at 2,000 ft. They point out that this result is satisfactory in view of the relatively small area that could be covered ; with the screen used in 1933 it would take 25 years of continuous flight and exposure to filter the air in one cubic mile, thus the chance of capturing larvae was unbelievably small when all things were taken into consideration.

Crosby & Bishop (1936) examined the spider material from Glick's* collections. Only those that could be identified are shown ; there were 900 tubes collected altogether, mostly of much damaged young spiders.

Hardy & Milne (1937), during a voyage on the research ship " George Bligh " from 5th to 13th August, 1936, flew kites with nets attached from the mast-head and from other parts of the ship. The altitudes varied from 200 to 400 ft. ; 730 insects were collected belonging to the following orders : Hemiptera, Diptera, Neuroptera, Trichoptera, and Lepidoptera. Some, mostly small-bodied insects, were found from 120–150 miles from land.

The same authors (1938 *a*) have published an extensive study of the distribution of insects by aerial currents. They investigated the atmosphere between the altitudes of 150 ft. and 2,000 ft. by collecting-nets carried up by kites. The nets were sent up closed, opened automatically at the desired height and closed again at the end of the sampling period before being hauled down. Eighty-two samples were taken numbering 839 insects during a total flying time of 124·5 hours. They state that the aerial plankton is made up essentially of small light-bodied insects with weak powers of flight, but with relatively large wing surface compared with body mass. Aphids formed 30 per cent. of the total insect catch, while together, the

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* See note Glick (P. A.) at end of this section.

TABLE VI.

(From Hardy and Milne, 1938 *a*.)

A. Numbers of Insects per 10-Hour Collecting at different Height-Ranges.

Height in feet	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneumonoidea	Chalcidoidea	Other Insects	Total
1,000–2,000 ...	2·4	14·4	0·0	11·2	1·6	4·0	1·6	0·0	1·6	2·4	4·8	44·0
750–1,000 ...	1·0	8·0	0·0	1·0	1·0	4·0	0·0	0·0	2·0	13·0	8·0	38·0
500–750 ...	5·0	16·5	2·0	0·0	1·0	4·5	0·5	2·0	4·0	2·5	10·5	48·5
250–500 ...	1·8	22·3	2·3	1·3	5·4	3·7	1·7	7·9	4·1	8·3	17·4	76·2
150–250 ...	0·8	28·6	8·2	0·0	40·0	0·8	7·3	16·3	3·3	0·0	11·6	116·9
Total	11·0	89·8	12·5	13·5	49·0	17·0	11·1	26·2	15·0	26·2	52·3	323·6

B. Percentage Composition of the Aerial Plankton within each Height-Range.

Height in feet	Jassidae	Aphididae	Staphylinidae	Chrysomelidae	Mycetophilidae	Chloropidae	Ephydridae	Other Acalypterae	Ichneumonoidea	Chalcidoidea	Other Insects	Total
1,000–2,000 ...	5·5	32·7	0·0	25·5	3·6	9·0	3·6	0·0	3·6	5·5	11·0	100
750–1,000 ...	2·4	21·1	0·0	2·6	2·6	10·5	0·0	0·0	5·2	34·2	21·4	100
500–750 ...	10·3	34·0	4·1	0·0	2·1	9·3	1·0	4·1	8·2	5·1	21·8	100
250–500 ...	2·4	29·3	3·0	1·7	7·1	4·9	2·2	10·4	5·4	10·9	22·7	100
150–250 ...	0·7	24·4	7·0	0·0	34·2	0·7	6·2	13·9	2·8	0·0	10·1	100

C. General Density of Aerial Plankton.

Height in Feet	Estimated No. of Insects in a Column of Air 1 mile sq.	Estimated No. of Insects Per 10^6 cu. ft.
1,000–2,000	245,000	9
750–1,000	65,000	9
500–750	72,000	10
300–500	104,000	18
150–300	123,000	29
10–150	339,000	87

Aphididae, Acalypterae, Mycetophilidae and Chalcidoidea, in order of their numerical importance, formed 65·5 per cent. of the total. This agrees in principle with Berland's findings. The figures (Table VI) taken from their paper give a general idea of the density and composition of the insect population of the upper air according to their sampling, only the more important families being given.

In a review of the contributed technical papers in connection with the U.S. Army Air Corps Stratosphere flight of 1935 in the balloon Explorer II (1938), a special spore-collecting apparatus was dropped from the balloon at 73,000 ft., and closed by means of syphon bellows at 36,000 ft., which is just about the base of the stratosphere. Bacteria and moulds were collected, 5 colonies of each being developed afterwards on agar jelly at 30°C.

Finally, Dr. J. A. Freeman has very kindly allowed the writer to quote from his unpublished work on " Studies in the Distribution of Insects by Aerial Currents " (see also Freeman, 1938). Dr. Freeman investigated on lines parallel to those of Hardy & Milne (1938), flying nets from the masts of the beam wireless station at Tetney, Lincolnshire. He specialised on the quantity and composition of the aerial fauna and flora from just above ground-level to nearly 300 ft. The drifting population above an area of agricultural land was sampled at heights of 10 ft., 177 ft. and 277 ft. over a front of 4,400 ft. ; 249 collections were made, 82 top, 84 middle and 83 bottom. They comprised 23,295 insects, 134 spiders, 157 mites, parts of plants and mineral debris. All the animals were alive and active when taken. The vast majority of insects were winged adults, but a number of wingless forms were taken included in the orders Collembola, Psocoptera, Hemiptera (nymphs) and Hymenoptera, in addition to Arachnida and Acarina. Very few strong-flying insects were taken, no bees or wasps, and very few large beetles, only one large Lepidopteron and that in a wind velocity of 35 m.p.h. Very few of the larger Calypterate Diptera occurred. Most of the insects collected may be regarded as forms which cannot fly strongly and are therefore unable to prevent themselves from being drifted by air currents. The numbers decreased with height, three-quarters being below 100 ft. Diptera were the most numerous below 100 ft., and Hemiptera above, apart from Aphididae which were dominant at all heights. Nine orders of insects were represented in the collection as follows:—Diptera 29 families, Hymenoptera 11 families, Hemiptera 10 families, Coleoptera 18 families, Thysanoptera 2 families, Lepidoptera 2 families, and Collembola, Psocoptera and Ephemeroptera, and in the

TABLE VII.

(From Freeman, unpublished.)

	Density (No. per 10^6 cu. ft.)			As percentages		
	277 ft.	177 ft.	10 ft.	277 ft.	177 ft.	10 ft.
Hemiptera	12·3	17·7	51·2	47·7	39·5	21·3
Diptera	5·4	11·6	100·4	20·9	26·1	41·9
Thysanoptera	1·2	2·5	2·6	4·6	5·7	1·0
Psocoptera	1·4	2·6	34·9	5·4	5·8	14·5
Coleoptera	1·8	3·5	11·9	7·1	7·8	4·9
Hymenoptera	3·6	6·7	39·2	13·8	14·9	16·3
Others	0·2	0·2	0·2	0·5	0·2	0·1
Total	25·9	44·8	240·4	100·0	100·0	100·0

Arachnida, 5 families of Araneidae and some undetermined Acarina. Table VII gives the mean densities and percentages of the various orders at each height.

Estimating the drifting aerial population Dr. Freeman states : " The idea of the actual number of insects drifted by the wind may be gathered from the calculation of the number of insects drifted per hour through a rectangle 300 ft. high and 1 mile broad, which is a little larger than the area actually bounded by the masts A and C. The average number drifted per hour was 12,500,000, of which 75 per cent. were below 100 ft. The maximum was 50,600,000 on 27.ix.34 and the minimum 457,900 on 23.viii.35. It is also of interest to note that even at the beginning (25.iii.35, 3,490,000) and at the end (1.xi.35, 1,500,000) of the year the numbers were high." It is interesting to compare these figures with Coad's.

The following table gives a comparison of the numbers of insects in the air, estimated as density in terms of numbers per 10^6 cu. ft. between Coad (1931), Hardy & Milne (1938) and Freeman (unpublished).

TABLE VIII.

Name	Height Range	Density (No. per 10^6 cu. ft.)
Coad	50–14,050	Jan. & May approx. average 80 for whole height range
Hardy & Milne ...	10–2,000	May to Oct. ,, ,, 27 ,, ,, ,,
Freeman ...	10–300	One year ,, ,, 103·7 ,, ,, ,,

Coad's figures are unexpectedly high in relation to altitude, as compared with the others, but this may be accounted for by the fact that he was using aircraft, as against the kites, and nets from wireless masts, used by the other two.

Table IX is a compilation from the records of Coad (1931), Berland (1935-36-37), Collins & Baker (1934), Crosby & Bishop (1936), Hardy & Milne (1938) and others. No record is given here the author of which is not mentioned in the text. As the purpose of this table is simply to indicate the type of insect population of the upper air the various records have not been assigned to their authors, and similarly if a family has been recorded at a given altitude by more than one author it is not duplicated.

It may reasonably be assumed that the atmosphere in most parts of the world contains a comparatively high population of insect life. The work of Coad, Berland, Hardy & Milne, Freeman and others, indicates that the atmosphere may, from the point of view of insect life, be divided into two zones, the " terrestrial " zone and the " plankton " zone or upper air. The first extends only to about 150 200 ft. and contains the greater majority of insects, including all those that by reason of their weight, strength and/or powers of flight are able to resist the upward convection currents of air, by means of which the " plankton " zone, which stretches from approximately 150–200 ft. to at least 14,000 ft. or more, is presumably populated.

. The " plankton " zone appears aptly named, as it contains a considerable population of small-bodied, weak-flying insects which float and drift in the upper air at the mercy of wind movement and vertical convection currents. This population is, within seasonal limits, probably fairly constant, but it is continually changing in its individual composition by the action of vertical currents in depositing large numbers of insects on land or sea, and with its constant replenishment from terrestrial sources by the same means.

Reference to Tables V and IX and to the literature will indicate the difference between collections made on house-tops, fire towers, etc., and those made with nets

TABLE IX.

Orders and Families of Insects caught in the Upper Air.

Height in Feet	Diptera	Hymenoptera	Coleoptera	Lepidoptera	Hemiptera		Psocoptera	Thysanoptera	Collembola	Araneida	Others
					Heteroptera	Homoptera					
7,500*	Chloropidae					Psyllidae					
6,500	Chloropidae					Psyllidae Aphidae					
6,000			Chrysomelidae								
5,000	Ephydridae					Psyllidae Aphidae		Thripidae		Argiopidae	
4,000	Ephydridae		Chrysomelidae			Psyllidae Aphidae Jassidae		Thripidae	Sminthuridae		
3,000 to 3,500	Cypselidae Cecidomyidae Ephydridae	Braconidae Chalcidae	Chrysomelidae			Psyllidae Aphidae Jassidae	Psocoptera	Adothripidae Tubulifera	Sminthuridae		
3,000	Culicidae†			Tineidae						Salticidae	
2,000 to 2,500	Cypselidae Cecidomyidae Ephydridae	Braconidae Chalcidae	Chrysomelidae			Psyllidae Aphidae	Psocoptera	Thysanoptera			
2,000	Lonchopteridae Chloropidae	Ichneumonidae Chalcidae	Carabidae Scolytidae	Lymantriidae						Dyctinidae Therediidae	
1,800	Ephydridae Chloropidae										
1,640	Heleidae Cypselidae Cecidomyidae Ephydridae	Braconidae Chalcidae				Psyllidae Aphidae					
1,500	Helomyzidae Chloropidae Ephydridae Sciaridae	Braconidae	Chrysomelidae			Jassidae Aphidae					

* Berland and Coad both consider that insects, mostly Aphids and small Diptera, as well as spiders, exist up to 14,000 ft. or over. Glick (1939) gives details of insects taken up to 15,000 ft.

† Felt (1925). The mosquito in question was *Aêdes dorsalis*, Meig., in swarms over the Central Sacramento Valley in 1919.

TABLE IX—*Continued.*

Orders and Families of Insects caught in the Upper Air.

Height in Feet	Diptera	Hymenoptera	Coleoptera	Lepidoptera	Hemiptera		Psocoptera	Thysanoptera	Collembola	Araneida	Others
					Heteroptera	Homoptera					
1,000	Ephydridae Chloropidae Chironomidae Borboridae Mycetophilidae Bibionidae Phoridae	Scelionidae Chalcidoidea Proctotrupoidea Ichneumonoidea	Scarabaeidae Chrysomelidae	Lymantriidae		Psyllidae Aphidae				Oecobiidae 1 undetermined	
700 to 900	Cecidomyidae Chloropidae Chironomidae Mycetophilidae Sciaridae	Ichneumonoidea Chalcidoidea Proctotrupoidea	Chrysomelidae			Jassidae Psyllidae Aphidae	Psocoptera	Thysanoptera			
700	Mycetophilidae Bibionidae	Ichneumonoidea Chalcidoidea	Staphylinidae			Psyllidae Aphidae	Psocoptera				
600	Chloropidae	Ichneumonoidea Chalcidoidea				Aphidae Psyllidae Jassidae		Thysanoptera		1 undetermined	
500	Agromyzidae Chloropidae Phoridae Ephydridae Empidae Chironomidae Cecidomyidae Mycetophilidae	Ichneumonidea Chalcidoidea Proctotrupoidea Cynipoidea	Scolytidae Heloidae Byrrhidae Carabidae Cucujidae	Pieridae Lymantriidae	Lygaeidae	Psyllidae Jassidae Aphidae Delphacidae		Thysanoptera		2 undetermined	
450	Agromyzidae Sphaeroceridae Chloropidae Drosophilidae Lonchopteridae Mycetophilidae	Proctotrupoidea Cynipoidea	Staphylinidae Chrysomelidae	Pieridae		Psyllidae Jassidae Aphidae Delphacidae		Thysanoptera			Coniopterygidae
400	Tipulidae Chloropidae Mycetophilidae	Ichneumonoidea Chalcidoidea				Psyllidae Aphidae Jassidae		Thysanoptera			

TABLE IX—*Continued.*

Orders and Families of Insects caught in the Upper Air.

Height in Feet	Diptera	Hymenoptera	Coleoptera	Lepidoptera	Hemiptera		Psocoptera	Thysanoptera	Collembola	Araneida	Others
					Heteroptera	Homoptera					
350	Bibionidae Ephydridae Cecidomyidae Mycetophilidae		Staphylinidae			Jassidae Aphidae Psyllidae		Thysanoptera			Trichoptera (1) (200–400 ft.)
300	Chloropidae Psychodidae Chironomidae Phoridae Agromyzidae Drosophilidae Empidae Cecidomyidae Mycetophilidae Syrphidae (200–400 ft.) Phoridae , ,, Acalyptrata ,, ,,	Proctotrypoidea Ichneumonoidea Chalcidoidea	Chrysomelidae Staphylinidae	Micro-lepidoptera (200–400 ft.)		Psyllidae Jassidae Aphidae		Thysanoptera		Spiders (6) (200–400 ft).	Hemerobiidae & Chrysopidae (200–400 ft.)
275	Rhyphidae Sphaeroceridae Muscidae Cordyluridae	Cynipoidea Proctotrupoidea	Hydrophilidae								
250	Chloropidae Mycetophilidae Rhyphidae	Ichneumonoidea Chalcidoidea	Chrysomelidae Staphylinidae			Aphidae Jassidae Psyllidae Delphacidae					
200	Mycetophilidae Agromyzidae Chironomidae Ephydridae	Ichneumonoidea Chalcidoidea	Staphylinidae			Aphidae Psyllidae					
175	Rhyphidae Muscidae					Aphidae					
150	Drosophilidae Sepsidae	Ichneumonoidea Chalcidoidea	Staphylinidae	Noctuidae (flew on board ship in North Sea)		Aphidae					

floated in the air by means of kites and aircraft. Although in some cases the altitudes at which the former were collected exceed the lower altitudes of the latter group, yet the former may broadly be described as " terrestrial " collections, while the latter pertain more to the " plankton " zone or upper air. Lienhart (1931) would seem to provide an exception, but the probability is that the insects which he found in the baskets of the balloons were able to make their entries either on the ascent or descent of the balloons owing to the relatively low speed at which these are made. This possibility, combined with the nature of the insects collected, would tend rather to emphasise the above-mentioned distinction.

It is interesting to note the absence of the Orthoptera from the " plankton " zone as well as the scarcity of Heteroptera, the non-occurrence of any insect or family of medical importance, and the inclusion of Odonata, Isoptera, Corrodentia and Megaloptera, etc., in the terrestrial collection. If the originals of Table V be consulted, it will be seen that the composition of the table in families and species is not only of much wider scope than that of the " plankton " zone, but includes many relatively large and heavy insects, thus bearing out the findings and theories of Berland, Hardy & Milne, and Freeman.

There can be little doubt that considerable movements of insect population are continually occurring through the agency of wind drift, and that many important pests have been spread by this means. It is impossible to combat, and quarantine regulations and means for their enforcement have frequently been thus set at nought by the forces of nature. Large scale dissemination of geographical faunistic groups is, however, prevented by the existence of natural barriers and their attendant adverse climatic conditions ; vast numbers of drifting insects have undoubtedly been destroyed by these means. The aeroplane may, and in the case of *Anopheles gambiae* in South America possibly has, overcome these barriers.

In view of the proved existence of a considerable aerial population, the question as to the possibility of aircraft collecting insects while in flight immediately arises. A comparison of Tables V and IX with the lists of insects taken in aircraft (Table X) reveals that the latter belong predominantly to the terrestrial group, and this together with the complete absence of any actual record of insects entering transport planes during flight would seem to indicate the improbability of such an occurrence.* This conclusion, as will be discussed later, is lent additional weight by a consideration of the design and construction of modern passenger-carrying aircraft.

Ability of Insects to survive Air Travel.

Various workers have conducted experiments to ascertain the ability of insects, particularly mosquitoes, to survive long distance air travel.

The work of Griffitts & Griffitts (1931) and Griffitts (1933, 1933 *a*) in Miami, Florida, using stained *Aëdes aegypti*, of Trolli (1932) using mosquitoes of the genus *Mansonia* and *Glossina palpalis*, in the Belgian Congo, and that of Hicks & Chand (1936) at Karachi also using female *A. aegypti*, has proved beyond doubt the ability of mosquitoes to endure journeys in aircraft of at least 9,580 miles in length and of 6½ days duration. Griffitts also proved that mosquitoes released in the cabins of aeroplanes would not necessarily leave the planes at intermediate stops. In addition Roubaud

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* Dr. P. A. Glick has just completed a paper on the results of his researches on the " Distribution of Insects, Spiders and Mites in the Air," initiated by Dr. Coad (1931). This paper (Tech. Bull. no. 673, U.S. Dept. Agric., Bur. Ent.) has just come to hand, unfortunately too late to be discussed here. Although his findings add considerably to the list of insects found in the upper air, his conclusions conform with the opinions expressed in this paper. He states " The size, weight and bouyancy of an insect contribute directly to the height to which it may be carried by air currents." With regard to aircraft as insect carriers he mentions instances of insects flying into the cockpits of his aeroplanes at 2,000 ft. and 4,000 ft. These were, however, apparently old-fashioned craft with open cockpits.

(1932) records that while experimenting with various European strains of *Anopheles maculipennis*, Mg., he was sent some specimens from Italy by air during the winter. They arrived frozen and apparently dead, but all revived completely when exposed to warmth and moisture.

Hicks & Chand (1936) also endeavoured to ascertain the reaction of mosquitoes to altitude and change of atmospheric pressure. They used an apparatus for testing altimeters consisting of two glass-fronted chambers, connected, and exhaustible simultaneously by a pump. The mosquitoes were enclosed in a glass tube covered with mosquito netting and could thus be observed. Altitudes of 5,000 and 10,000 ft. were tested, taking 25 and 50 seconds and 10 and 30 minutes to reach, remaining at that pressure for 1 and 3 minutes and 1 and 3 hours. The times of descent were 10 and 12 seconds and 10 and 30 minutes. In no case were the mosquitoes inconvenienced.

The writer, working in collaboration with the late Prof. H. M. Lefroy, carried out some experiments in 1924 upon the ability of insects to withstand varying pressures and vacuums. A specially built iron cylinder was used with pressures up to 150 lb. per square inch, but records of the degrees of vacuum reached have unfortunately been lost. Various types of insects were tested, including *Musca domestica*, Lepidopterous larvae, and adult Tenebrionids. The experiments were repeated with the insects' spiracles sealed by means of wax. Both pressure and vacuum were released suddenly, and maintained for periods up to 24 hours. In no case did any insect show signs of distress.

These results are borne out by various Imperial Airways Captains who have informed the writer that on occasions the descent from high altitudes (12,000 ft. or more) and low temperatures has been most rapid, with no apparent effect upon the insects subsequently found in the planes.

The conclusion that mosquitoes are able to withstand long and varied journeys in aircraft is amply confirmed by the records of insects found in aircraft (Table X). It is interesting, however, to note in this connection that Pemberton (1938) concludes from tests made with 400 adult sugar-cane leaf-hoppers, that rarely, if ever, would these insects survive the 48-hour trip from Samoa to Honolulu without food.

Insects found in Aircraft: World Results (Table X).

Insects must have been noticed in aircraft by pilots for very many years, but unfortunately no records were kept in the early days of commercial aviation. The earliest instance known to the writer is that of Mr. J. S. Newall, who in 1927 was flying a D.H. 96 in India. He states that he has had a number of rats in his planes as well as unidentified insects found at the end of a flight, and on one occasion a rat which was being chased in the hangar escaped into the aeroplane and disappeared. About one month later Mr. Newall noticed that his maps and the elastic of his goggles were being eaten, and on ordering an investigation found a rat's nest snugly ensconced in the fuselage towards the tail. Mr. C. G. Lumsden, late of Imperial Airways, has often noticed insects in his flying boats, and on one occasion, about the end of 1932, discovered a bird's nest containing an egg in the nascelle* of one of the engines of a 3-engined Short Calcutta flying boat. The craft in question had been laid up for a week for overhaul, and during this time the nest must have been built and the egg laid. Mr. Lumsden brought the boat from Kisumu to Khartoum with both nest and egg *in situ* and without damage to either.

A number of workers have investigated insects found in aircraft, but with one exception they have concentrated upon mosquitoes, with the result that much valuable information has been lost. Table X gives a complete list of insects taken in aircraft,* but there are certain points impossible to include in a table which are of interest.

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* The nascelle was a hollow streamlined cone behind the radial engine designed to reduce wind drag.

The first record of insects carried by aircraft appears to be that of Kisliuk (1929), who states that on the arrival, in October 1928, of the Graf Zeppelin on her first commercial voyage to the United States, three bunches of flowers, one of roses, one of chrysanthemums and one of carnations, were discovered in the possession of passengers, and on these were found Aphids, Coccids, thrips, and eggs and a cocoon of a Noctuid moth, and an unidentified spider. He does not mention if the airship itself was searched for insects.

Griffitts & Griffitts (1931) made 102 inspections, between 23rd July and 12th September, 1931, of aeroplanes arriving at Miami, Florida, from localities in South and Central America, Mexico and the West Indies. A total of 29 mosquitoes were captured from 21 machines.

Trolli (1932 and 1932 *a*) collected mosquitoes from aircraft in the Belgian Congo ; he considered that the mosquitoes were introduced at the intermediate stops and not at night stations.

James (1934) referring to observations made in Kenya by Symes states that of 30 aeroplanes examined at Kisumu and Nairobi, 18 harboured mosquitoes, generally 2–6, but once, after a forced landing, as many as 23.

Symes (1935) presented the results of his collections in aircraft arriving at Kisumu and Nairobi, a summary of part of which had already been published by James (1934) together with some other results. During the period June to the end of December 1933, 25 aeroplanes from Juba and Entebbe were searched, 10 containing insects. During 1934, at Kisumu, 52 aeroplanes from the north were searched, of which 23 contained insects, and from the south 52 were searched, 12 containing insects ; and at Nairobi the figures were, from the north 26 and 4 and from the south 41 and 8.

Hicks & Chand (1936) searched aeroplanes arriving at Karachi airport, but found no mosquitoes ; they do not mention if other insects were present.

During November 1936 the Public Health Service at Miami (Mosquitoes on Airplanes, 1937) made 69 inspections of aircraft. In 24 cases, 53 insects were captured. In 7 of these 13 mosquitoes were found of which 2 were dead ; the maximum number of mosquitoes on any one aeroplane was 3, of which 2 were dead.

Dr. Park Ross (Ross 1938) gives a short list of insects found in aircraft at Durban Airport during 1937 and 1938 and has also been kind enough to send the writer the MS. of part of his paper on this subject shortly to be published. The following figures have been compiled from Dr. Park Ross's letters, the Durban Port Officer's returns and from his afore-mentioned paper.

Of the 171 planes that arrived, live insects were found in 50, dead insects in 38, and none in 83.

In the 94 planes sprayed by the crews, live insects were found in 30, dead insects were found in 26, and none in 38.

In the 77 planes not sprayed by the crews, live insects were found in 20, dead insects in 12, and none in 45.

Describing the routine destruction and collection of insects Dr. Park Ross states, " At the Marine Airport of Durban the following procedure has been practised since the inception of the flying boat service in 1937. As it differs in detail from most other ports I give it in full.

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* There have been collections of insects from aircraft arriving at Miami during 1937, and possibly earlier, of which no results have, to the writer's knowledge, been published.

"(*a*) Arrivals of planes is awaited by Port Health Officer, European Sanitary Inspector and one native assistant.

"(*b*) Incoming planes have to keep all hatches and openings (except mooring hatch) closed until P.H.O. gives permission to open. This is strictly enforced.

"(*c*) On signal from P.H.O. and not before, forward hatch is opened to permit entrance of Port Health Staff, Customs and Imperial Airways officials. This hatch and the door leading to passenger accommodation are then closed.

"(*d*) Spraying begins at once and compartments are dealt with in the following order :—Lavatories, pantry, passage, lower forward freight, anchor room, pilot's cockpit, and upper mail compartment, after which the sanitary inspector and native assistant pass through the cabin to deal with the rear baggage compartment.

"(*e*) During the spraying process the usual business incidental to disembarkation is carried on by Airways and other departmental officials, provided doors are kept shut as shown.

"(*f*) Eight minutes after spraying the forward compartments, corridor and cabin doors are opened to allow passengers to proceed via the forward cabin to awaiting launch.

"(*g*) Discharge of mails and baggage is begun 8 minutes after respective compartments are sprayed.

"(*h*) Immediately passengers have left, corridors are shut and cabin fumigation begins. It is completed in eight minutes, after which the plane is completely opened up.

"(*i*) After spraying a 15 minutes search is made and results are recorded."

Unfortunately the insects collected have only been roughly classified and very few scientific identifications have been made. The writer understands that the full-time services of an entomologist were not available.* Dr. Park Ross emphasizes that the hand-spraying by crews using flit guns and an undetermined insecticide continues to be unreliable.

Welch (1939) is the only worker to pay attention to insects other than those of medical importance. His report lists the insects captured during routine quarantine inspections on sea-planes arriving at Pan American Airport, Dinner Key, Miami, Florida, from Central and South America, Mexico and the West Indies during 1938. Describing the methods of search he states : " Immediately upon arrival the planes are placed in quarantine and, after disembarkation of passengers and crew, are boarded for inspection. A time limit of 6 minutes is set for the inspection of each plane before the unloading crew is permitted to come aboard. During this 6-minute period, searches are made in the passenger and pilot compartments. The mail, express and baggage compartments are inspected during and after unloading, as these compartments are kept closed during flight and until time of unloading of the plane. Inspections are made without the benefit of any mechanical devices other than flashlight and glass chloroform tubes . . . . Disinsectization of aircraft is performed by employees of the airways. The plane is sprayed in the air by the steward, one half hour before landing at Miami and other ports of call en route, with an atomiser sprayer (small hand pump gun) charged with a spraying fluid consisting of one part of a standardised pyrethrum extract containing 2 grams of pyrethrin per 100 cc., and 4 parts of a highly refined mineral oil having a relatively high flash point. During the time of spraying, the plane's ventilators are closed and are kept closed for approximately 10 minutes after spraying. An effort is made to spray thoroughly all compartments of the plane, using between 5 and 10 c.c. of the insecticide per 1,000 cu. ft. On overnight stops the planes are thoroughly sprayed after disembarkment of passengers and crew, and the plane is closed for the night."

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* Dr. Park Ross was primarily engaged upon investigating the control of insects in aircraft.

A record is kept of all insects collected in the planes, which affords a quarantine check on the effectiveness of disinfection of the planes. His figures are as follows :—398 aircraft were inspected during the year, 187 being found to harbour dead and alive insects ; 651 insects were recovered, of which 166 were alive when captured ; 45 mosquitoes were found, of which 5 were alive.

The author points out that, in spite of the precautions taken by the Airways and health authorities, live mosquitoes and other insects are still being transported into America by aircraft. The figures would appear to substantiate Park Ross's opinion as to the inefficacy of the flitting of planes by the crew with hand-pump "flit guns."

It is a matter of regret that Welch's paper is marred by inaccuracies and inconsistencies ; thus he gives in the general portion of his table of insects found, which includes all records, the figure 274 for *Chironomus* spp., while later in the sections under route headings this same entry is given as 300. Puzzling entries are made such as *Euxesta notata* (fruit fly) and ditto (gnat) ; while *Drosophila melanogaster* is termed a fruit fly, *D. repleta* is called a gnat, and *D. melanica* (?) a small fly. The spelling is incorrect in certain instances, and surprisingly, for an entomologist, the cockroaches are classified under the Hemiptera. These inaccuracies have been amended in Table X.

Insects Found in Commercial Aircraft arriving at Khartoum Airport, July 1935-August 1938.

The work was started in July 1935, and continued without a break until 31st August 1938. During the period 30.v.36 to 23.viii.36, while the writer was on leave, the material coming from all parts of the country, including the insects collected from aircraft, was, owing to the inefficiency of a subordinate, allowed to accumulate in tubes as handed in, with the result that when, upon the writer returning from leave, the material was examined, much of it was found to be indeterminable. This unfortunately resulted in a large number of records of insects from aircraft being lost.

Khartoum is an important air junction, and commercial aircraft from South Africa, West Africa, Eritrea and Cairo, make it a night stop or terminus. Khartoum is seldom used as a frontier port, and aircraft alighting there have for the most part already submitted to customs and quarantine examinations at one of the entry ports. These are, for the north, Wadi Halfa ; for the south, Juba for land planes, Malakal for flying boats ; for the east, Kassala ; and for the west, either Geneina or Fasher. Aircraft entering the Sudan are sprayed for insects at the entry ports.

Owing to the fact that all commercial aircraft made Khartoum a night stop, plenty of time was available for investigation. To begin with the planes were thoroughly sprayed on arrival by means of a hand "flit gun," using a commercial pyrethrum spray "Shelltox" or "Flit," and the dead insects were subsequently collected for examination. This was found to result in so much damage to the insects that many of them were indeterminable, so the following method was evolved ;

glass tubes 3 in. by 1 in. or 4 in. by 1 in., were prepared with cottonwool soaked in " Shelltox " or " Flit," which was covered by a perforated cardboard disc in order to prevent small and delicate insects from coming into contact with the cotton wool and so getting damaged. Wherever possible insects were caught by means of the tubes, but elusive specimens were stunned by a puff from the " flit " gun and then placed in tubes. The " flit " tubes were not strong enough to kill all insects, and many of them were still alive when received in the laboratory. By these means damage to material was reduced to a minimum. The aim of the searchers was not to disinfect the aircraft, but to collect all insects found in them.

The first one or two investigations were carried out by the writer for experimental purposes, after which the Sanitary Department of the Sudan Medical Service took over. The procedure was as follows :—A British or native sanitary inspector, accompanied by two searchers, met each plane. Passengers were allowed to disembark with their luggage, and a close watch was kept upon the door in the side of the plane in case any insects escaped while it was open. The sanitary squad then entered the plane, closed all doors and windows, and began their search. The " flit " gun was used to dislodge insects from hiding-places, and no time limit was set, as the primary object was the collection of insects. It should be emphasised that patience and plenty of time are essential in undertaking collecting work of this nature, it being the writer's opinion that the time limits mentioned by Park Ross and Welch are inadequate for collecting purposes. Owing to the complexity of the interior arrangements of even the largest and most modern aircraft, little benefit was obtained from the employment of extra staff. Customs and mail staff had to wait until the search was completed ; sometimes this took well over half an hour.

Up to the beginning of 1936 one of the commercial pyrethrum insecticides " Shelltox " or " Flit " was used, but since February 1936 a special formula evolved by the collaboration of the S.M.S. and the Government Entomologist, Mr. H. W. Bedford, was employed, as follows :—

Pyrethrum extract	5·8 per cent.	by volume.
Essence of citronella	2·0 ,, ,,	
Carbon tetrachloride	49·0 ,, ,,	
Kerosene	43·2 ,, ,,	

This mixture has the advantage of being economical and practically non-inflammable, and for the purposes for which it was used, adequate. For reasons which will be discussed later, the writer would not advocate its use for the control of insects in aircraft on a large scale. While every precaution was taken in order to make the search as complete and effective as possible, there is little doubt that insects were occasionally missed.

Insects were generally found in the main cabins of the various aircraft, but occasionally specimens were collected from the baggage compartments. The exact localities of the insects varied according to type, some being found on the window-panes, others in the folds of curtains, in crevices, corners, under shelves, etc., and some flying about the cabin. Mosquitoes were usually found under the seats and in dark corners.

Within limits all aircraft arriving at Khartoum airport from outside the Sudan were examined. It was, however, owing to the limited staff, impossible to compete with all the movements of military craft, and occasional transcontinental flyers and record breakers would turn up unannounced. In no case were insects found in private or military aircraft.

World List of Insects found in Aircraft.

The following table comprises all records of insects taken in aircraft. Richards (1938) published a preliminary list of mosquitoes found in aircraft arriving at

Khartoum airport, compiled largely from data supplied by the writer. These were, at the time, only identified to genera, the majority being in very bad condition, but some have since been determined. These records are included in this table.

The following are descriptions of the aircraft in which collections have been made, and the abbreviations used for them in the table :—

Africa.

H.P.H.=Handley-Page " Hannibal " Class ; 4-motor multi-seater biplane, cruising at 85–100 m.p.h. Now obsolete.

E.F.B.=Short Bros. " Empire Flying Boat " ; 4-motor 22-seater monoplane, or 17-seater+4,400 lb. of mails and freight, or variations, cruising at 160 m.p.h.

D.H. 86=De Haviland 4-motor 10-seater+395 lb. of baggage or variations, biplane, cruising at 140 m.p.h.

S-M.=Savoia-Marchetti 3-motor multi-seater monoplane, cruising at 160 m.p.h.

Atalanta=Armstrong-Whitworth " Atalanta " 4-motor multi-seater monoplane, cruising at 130 m.p.h.

H.P.=Handley-Page. Type not specified.

Fokker=Fokker. Type not specified.

N.B.—The cruising speeds given are approximate only; they may vary considerably with weather conditions. Other information is as accurate as possible, but seating details, etc., may be varied in different areas to suit local conditions.

Central and South America.

S.4=Sikorsky " Clipper " ; 4-motor, 12-ton, 32 passenger flying boat, cruising at 150 m.p.h. (approximately).

S.2=Sikorsky " Baby Clipper " ; 2-motor, 6-ton, 13 passenger flying-boat.

S.=Sikorsky 2-motor flying-boats, details unknown. Probably now obsolete.

The numbers in column 1 refer to species, not necessarily identified as such, but distinguishable by reason of family or genus from the named species. Insects of the same genus distinguishable from each other as separate, although unknown species, are similarly allotted numbers. Only those records which are completely unidentifiable are given no numbers, and are grouped under the heading " Unidentified "

Abbreviations of authors' names in column 3.

Welch =Welch, E. V. (1939).
Symes =Symes, C. B. (1935).
,, (*a*) = ,, ,, (1937).
G. & G. =Griffitts, T. H. D. & Griffitts, J. J. (1933).
G. =Griffitts, T. H. D. (1933).
Ross =Ross, G. A. Park (1938).
,, (*a*) = ,, ,, ,, (unpublished).
P.H.S. =Public Health Service, Miami (Mosquitoes on Airplanes, 1937).
Trolli =Trolli, G. (1932).
,, (*a*) = ,, ,, (1932 *a*).
Michel =Michel in " Sur la destruction des Moustiques à bord des aéronefs (1935).
Orig. =Original.

TABLE X.

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus†.

No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Diptera							
	Mycetophilidae							
1	Sciara sp.	Welch	10	3	1938	Miami	Barranquilla	S.4
	,, ,,	,,		2	,,	,,	Rio de Janeiro	,,
	,, ,,	,,		2	,,	,,	Port of Spain	,,
	,, ,,	,,		3	,,	,,	San Juan	,,
	Bibionidae							
2	Dilophus orbatus, Say	,,	1		,,	,,	Barranquilla	,,
	Simuliidae							
3	Simulium sp.	Orig.	9		1.2.36	Khartoum	Cairo	H.P.H.
	Ceratopogonidae							
4	Dasyhelea sp.	Welch	1		1938	Miami	Port of Spain	S.4.
5	Forcipomyia sp.	,,	5	1	,,	,,	Barranquilla	,,
	,, ,,	,,		3	,,	,,	Port of Spain	,,
	,, ,,	,,		1	,,	,,	Cristobal	,,
6	Culicoides sp.	,,	1		,,	,,	Maracaibo	,,
	Chironomidae							
7	Chironomus sp.	Orig.	40	3	8.2.36	Khartoum	Cairo	H.P.H.
	,, ,,	,,		5	28.3.38	,,	,,	E.F.B.
	,, ,,	,,		1	29.3.38	,,	,,	,,
	,, ,,	,,		2	8.2.36	,,	Cape Town	H.P.H.
	,, ,,	,,		2	14.1.36	,,	,,	,,
	,, ,,	,,		2	10.7.38	,,	Durban	E.F.B.
	,, ,,	,,		4	16.7.38	,,	,,	,,
	,, ,,	,,		2	22.7.38	,,	,,	,,
	,, ,,	,,		2	26.7.38	,,	,,	,,
	,, ,,	,,		2	25.1.36	,,	Asmara	S-M.
	,, ,,	,,		1	27.7.36	,,	,,	,,
	,, ,,	,,		3	30.7.36	,,	,,	,,
	,, ,,	,,		1	6.8.36	,,	,,	,,
	,, ,,	,,		2	8.8.36	,,	,,	,,
	,, ,,	,,		4	13.8.36	,,	,,	,,
	,, ,,	,,		2	17.9.36	,,	,,	,,
	,, ,,	,,		1	1.10.36	,,	,,	,,
	,, ,,	,,		1	30.11.36	,,	,,	,,
	,, ,,	Symes	1		1934	Kisumu	South	H.P.H.
	,, ,,	Welch	300		1938	Miami	Maracaibo	S.4.
	,, ,,	,,	1		,,	,,	San Juan	S.2.
8	Clinotanypus sp.	Orig.	1		14.1.36	Khartoum	Cape Town	H.P.H.
9	,, ,,	Welch	1		1938	Miami	Maracaibo	S.4
10	Pentaneura sp.	,,	10		,,	,,	,,	,,
	Unidentified Chironomidae	Symes	2		1934	Kisumu	North	H.P.H.
	,, ,,	,,	1		8-12/33-34	Nairobi	South	,,
	,, ,,	Ross (*a*)	3		1938	Durban	North	E.F.B.
	Culicidae							
11	Anopheles gambiae, Giles†	Orig.	1		24.3.37	Khartoum	Capetown	H.P.H.
	,, ,, ,,	,,	1		7.10.36	,,	,,	,,
	,, ,, ,,	Symes	21		6.12.33	Kisumu	Juba & Entebbe	H.P.H.
	,, ,, ,,	,,	3		,,	,,	North	,,
	,, ,, ,,	,,	3		8-12/33-34	Nairobi	,,	,,
	,, ,, ,,	,,	1		,,	,,	South	,,

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus †.

No. of spp.	Insect	Author	No. of insects	Date	Where collected	Plane From	Type of plane
	Diptera—*Cont.* CULICIDAE—*Cont.*						
12	A. funestus, Giles	Orig.	1	2.6.36	Khartoum ...	Capetown ...	H.P.H.
	,, ,, ...	Symes	32	6-12/33	Kisumu ...	Juba & Entebbe	H.P.H. ?
	,, ,, ...	,,	6	1934	,, ...	North	,,
	,, ,, ...	,,	6	8-12/33-34	Nairobi ...	,, ...	,,
13	A. pharoensis, Theo. ...	Orig.	2	28.9.36	Khartoum ...	Capetown ...	H.P.H
14	A. mauritianus, Grp. ...	,,	1	11.8.36	,, ...	,, ...	,,
15	A. albimanus, Wied. ...	G. & G.	some	1931-32	Miami ...	Central & South America & West Indies	S. ?
	,, ,, ...	Welch	1	1938	,, ...	Maracaibo ...	S.4
16	A. pseudopunctipennis, Theo.	G.	some	7-9/31	,, ...	Central & South America & West Indies	S. ?
	Unidentified Anopheles ...	Orig.	5 1	1.8.35	Khartoum ...	Cairo	H.P.H.
	,, ,, ...	,,	1	15.8.35	,, ...	,, ...	,,
	,, ,, ...	,,	2	20.8.35	,, ...	Tripoli	S-M.
	,, ,, ...	,,	1	18.9.35	,, ...	Cairo	H.P.H.
	,, ,, ...	,,	5	24.3.37	,, ...	Asmara ...	S-M.
	,, ,, ...	Ross	2 times	1937	Durban ...	North	E.F.B.
		,, (*a*)	4 times	1938	,, ...	,, ...	,,
17	Theobaldia longiareolata, Macq.	Orig.	4 1	25.2.36	Khartoum ...	Lagos	D.H.86
		,,	1	14.3.36	,, ...	Asmara ...	S-M.
	,, ,, ,,	,,	1	24.1.36	,, ...	,, ...	,,
	,, ,, ,,	,,	1	10.9.36	,, ...	,, ...	,,
18	Mansonia africana, Theo.*	,,	1	20.10.35	,, ...	Cairo	H.P.H.
19	M. uniformis, Theo.† ...	,,	1	11.8.36	,, ...	Asmara ...	S-M.
20	M. titillans, Wlk.† ...	Welch	1	1938	Miami ...	Barranquilla ...	S.4
	,, ,, ...	G. & G.	examples of	7-9.31	,, ...	Central & South America & West Indies	S. ?
	,, ,, ...	P.H.S.	3	11.36	,, ...	,, ,, ,,	,,
21	M. indubitans, Dyar & Shannon	,,	1	,,	,, ...	,, ,, ,,	,,
	,, ,, ,,	Welch	19	1938	,, ...	Barranquilla ...	S.4
	Unidentified Mansonia ...	Trolli (*a*)	9	1932	Leopoldville	Stanleyville ...	H.P. ? Fokker ?
	,, ,, ...	,,	4 1	10.4.31	Coquilhatville	Lisala-Leopoldville	,,
	,, ,, ...	,,	3	19.5.31	,, ...	,, ,,	,,
	,, ,, ...	Welch	1	1938	Miami ...	Port of Spain ...	S.4
	,, ,, ...	Orig.	14	20.10.35	Khartoum ...	Cairo ...	H.P.H.
22	Aëdes lineatopennis, Ludl.	,,	1	11.8.36	,, ...	Asmara ...	S-M.
23	A. luteocephalus, Newst.*	,,	1	30.8.36	,, ...	,, ...	,,
24	A. simpsoni, Theo.* ...	,,	1	,,	,, ...	Capetown ...	H.P.H.
25	A. furcifer, Edw.	,,	1	,,	,, ...	,, ...	,,
26	A. ochraceus, Theo. ...	,,	1	11.8.36	,, ...	,, ...	,,
27	A. taeniorhynchus, Wied.*	G. & G.	some	1931-32	Miami ...	Central & South America & West Indies	S. ?
	,, ,, ...	Welch	7 2	1938	,, ...	Barranquilla ...	S.4
	,, ,, ...	,,	1	,,	,, ...	Cristobal ...	,,
	,, ,, ...	,,	1	,,	,, ...	Maracaibo ...	,,
	,, ,, ...	,,	2	,,	,, ...	Port of Spain ...	,,
	,, ,, ...	,,	1	,,	,, ...	San Juan ...	S.2

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus †.

No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Diptera—*Cont.* CULICIDAE—*Cont.*							
28	A. nigeriensis, Theo. ...	Symes & Roberts	1		1935	Kenya		
29	A. argenteopunctatus, Theo.	,,	1		,,	,,		
30	A. sollicitans, Wlk. ...	P.H.S.	1		11.36	Miami ...	Central & South America & West Indies	S. ?
31	A. aegypti, L.	Orig.	2		2.37	Malakal ...	Juba	H.P.H. ?
	,, ...	G. & G.	1		28.7.31	Miami ...	San Salvador ...	S. ?
	Unidentified Aëdes ...	Ross	twice		1937	Durban ...	North ...	E.F.B.
	,, ,, ...	,, (*a*)	once		1938	,, ...	,, ...	,,
	,, ,, ...	Trolli (*a*)	1		1932	Leopoldville	Stanleyville ...	H.P. ?
32	Culex fatigans, Wied.* ...	Orig.	1		18.7.36	Khartoum ...	Cairo	H.P.H.
	,, ,, ,, ...	G. & G.	28		7-9.31	Miami ...	Central & South America & West Indies	S. ?
	,, ,, ,, ...	P.H.S.	3		11.36	,, ...	,, ,,	,,
	,, ,, ,, ...	Welch	9	1	1938	,, ...	Barranquilla ...	S.4
	,, ,, ,, ...	,,		1	,,	,, ...	Rio de Janeiro	,,
	,, ,, ,, ...	,,		6	,,	,, ...	Port of Spain ...	,,
	,, ,, ,, ...	,,		1	,,	,, ...	San Juan ...	S.2
33	C. poecilipes, Theo. ...	Orig.	4	1	8.8.36	Khartoum ...	Asmara ...	S-M.
	,, ,, ...	,,		1	11.8.36	,, ...	Capetown ...	H.P.H.
	,, ,, ...	,,		1	28.5.37	,, ...	Asmara ...	S-M.
	,, ,, ...	,,		1	3.6.37	,, ...	,, ...	,,
34	C. tigripes, Grp.	,,	1		28.9.36	,, ...	,, ...	,,
35	C. theileri, Theo.	,,	1		18.6.36	,, ...	,, ...	,,
36	C. inhibitator, D. & K. ...	P.H.S.	1		11.36	Miami ...	Central & South America & West Indies	S. ?
	Unidentified Culicines ...	Orig.	63		1935-36	Khartoum ...	Asmara ...	S.M.
	,, ,, ...	,,	1		1937	,, ...	,, ...	,,
	,, ,, ...	,,	7	6	,,	,, ...	Cairo & Tripoli	H.P.H. & S-M.
	,, ,, ...	,,		1	1935-36	,, ...	Capetown ...	H.P.H.
	,, ,, ...	Symes	73		1933	Kisumu ...	Juba & Entebbe	H.P.H. ?
	,, ,, ...	,,	6		1934	,, ...	North	,,
	,, ,, ...	,,	4		1934	,, ...	South	,,
	,, ,, ...	,,	1		8-12/33-34	Nairobi ...	North	,,
	,, ,, ...	,,	1		,, ,,	,, ...	South	,,
	,, ,, ...	P.H.S.	1		11.36	Miami ...	Central & South America & West Indies	S. ?
	,, ,, ...	Welch	6	1	1938	,, ...	Barranquilla ...	S.4
	,, ,, ...	,,		4	,,	,, ...	Rio de Janeiro	,,
	,, ,, ...	,,		1	,,	,, ...	San Juan ...	S.2
	,, ,, ...	Ross	5 times		1937	Durban ...	North	E.F.B.
	,, ,, ...	,, (*a*)	twice		1938	,, ...	,, ...	,,
	,, ,, ...	Trolli	6	1	3.3.31	Leopoldville	Lisala-Stanleyville	H.P. ?
	,, ,, ...	,,		2	10.4.31	,, ...	,, ,,	,,
	,, ,, ...	,,		3	25.5.31	,, ...	,, ,,	,,
	,, ,, ...	,, (*a*)	5		1932	,, ...	Stanleyville ...	,,

TABLE X—*Continued.*

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus †.

No. of spp.	Insect	Author	No. of insects	Date	Where collected	Plane from	Type of plane
	Diptera—*Cont.*						
	CULICIDAE—*Cont.*						
37	Psorophora ciliata, F.	G.	some	1931-32	Miami	Central & South America & West Indies	S. ?
38	P. columbiae, D. & K.	,,	,,	,,	,,	,, ,,	,,
39	Chaoborus sp.	Welch	15	1938	,,	Maracaibo	S.4
	Unidentified Culicidae	P.H.S.	some	11.36	,,	Central & South America & West Indies	S. ?
	,, ,,	Ross (*a*)	,,	1938	Durban	North	E.F.B.
	,, ,,	Welch	1	,,	Miami	Barranquilla	S.4
	TIPULIDAE						
40	Limonia sp.	,,	1	,,	,,	,,	,,
	STRATIOMYIIDAE						
41	Euryneurasoma slossonae, Johns.	,,	1	,,	,,	Cristobal	,,
	TABANIDAE						
42	Tabanus taeniola, P. de B.	Orig.	28 2	17.5.36	Khartoum	Capetown	H.P.H.
	,, ,, ,,	,,	1	22.9.37	,,	Durban	E.F.B.
	,, ,, ,,	,,	1	1.10.37	,,	,,	,,
	,, ,, ,,	,,	1	31.10.37	,,	,,	,,
	,, ,, ,,	,,	1	3.11.37	,,	,,	,,
	,, ,, ,,	,,	1	5.11.37	,,	,,	,,
	,, ,, ,,	,,	2	10.11.37	,,	,,	,,
	,, ,, ,,	,,	3	12.11.37	,,	,,	,,
	,, ,, ,,	,,	1	19.11.37	,,	,,	,,
	,, ,, ,,	,,	1	24.11.37	,,	,,	,,
	,, ,, ,,	,,	2	3.12.37	,,	,,	,,
	,, ,, ,,	,,	1	8.12.37	,,	,,	,,
	,, ,, ,,	,,	2	10.12.37	,,	,,	,,
	,, ,, ,,	,,	2	15.12.37	,,	,,	,,
	,, ,, ,,	,,	2	17.2.37	,,	,,	,,
	,, ,, ,,	,,	3	19.12.37	,,	,,	,,
	,, ,, ,,	,,	1	26.12.37	,,	,,	,,
	,, ,, ,,	,,	1	26.1.38	,,	,,	,,
43	T. fasciatus niloticus, Aust.	,,	4 2	12.11.37	,,	,,	,,
	,, ,, ,,	,,	1	3.12.37	,,	,,	,,
	,, ,, ,,	,,	1	8.12.37	,,	,,	,,
44	Haematopota taciturna, Aust.	,,	1	1.10.37	,,	,,	,,
45	Chrysops longicornis, Macq.	,,	1	28.7.38	,,	,,	,,
46	Chrysops distinctipennis, Aust.	,,	1	28.7.38	,,	,,	,,
	Unidentified Tabanidae	Symes	18	6-12.33	Kisumu	Juba & Entebbe	H.P.H. ?
	,, ,,	,,	6	1934	,,	North	,,
	,, ,,	Ross	some	1937	Durban	,,	E.F.B.
	THEREVIDAE						
47	Salentia rufofemorata, Hartig	Orig.	2 1	23.6.37	Khartoum	Lagos	D.H.86
			1	2.7.37	,,	,,	,,
48	Psilocephala sp.	Welch	1	1938	Miami	Merida	S.2

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus †.

No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Diptera—*Cont.*							
	SCENOPINIDAE							
49	Scenopinus sp.	Welch	1		1938	Miami	Cristobal	S.4
	EMPIDAE							
50	Hybos sp.	,,	1		,,	,,	Barranquilla	,,
51	Drapetis sp.	,,	3		,,	,,	,,	,,
	DOLICHOPODIDAE							
52	Medetera sp.	,,	1		,,	,,	,,	,,
53	Chrysotus sp.	,,	2	1	,,	,,	Maracaibo	,,
	,,	,,		1	,,	,,	Barranquilla	,,
54	Pelastoneurus sp.	,,	1		,,	,,	,,	,,
	PHORIDAE							
55	Megaselia sp.	,,	3	1	,,	,,	,,	,,
	,,	,,		1	,,	,,	San Juan	S.2
	,,	,,		1	,,	,,	Merida	,,
	TACHINIDAE							
56	Sturmia inconspicua, Hartig.	Orig.	2	1	23.6.37	Khartoum	Lagos	D.H.86
	,, ,, ,,	,,		1	2.7.37	,,	,,	,,
	CALLIPHORIDAE							
57	Sarcophaga hirtipes, Wied.	,,	2		13.12.37	,,	Cairo	E.F.B.
58	S. setinervis, Rond.	,,	1		28.9.36	,,	Asmara	S-M.
59	S. sp.	,,	1		25.9.36	,,	,,	,,
60	S. sp.	,,	3	1	14.9.36	,,	,,	,,
	,,	,,		1	13.3.37	,,	,,	,,
	,,	,,		1	11.8.38	,,	,,	,,
61	Chrysomyia albiceps, Wied.	,,	1		24.3.37	,,	,,	,,
62	Tricyclea sp.	,,	1		——	,,	,,	,,
	MUSCIDAE							
63	Lyperosia minuta, Bezzi	,,	3	1	28.7.38	,,	Durban	E.F.B.
	,, ,, ,,	,,		2	26.11.35	,,	Cairo	H.P.H.
64	Atherigona orientalis, Schin.	Welch	1		1938	Miami	Cristobal	S.4.
65	Synthesiomyia nudiseta, Wulp.	,,	1		,,	,,	Barranquilla	,,
66	Philaematomyia crassirostris, Stein	Orig.	5	1	28.9.36	Khartoum	Asmara	S-M.
	,, ,,	,,		1	24.11.36	,,	Capetown	H.P.H.
	,, ,,	,,		1	20.4.37	,,	,,	,,
	,, ,,	,,		2	24.4.37	,,	,,	,,
67	Stomoxys calcitrans, L.*	,,	35		1935–1938	,,	All parts	All types
	,, ,,	Welch	3	1	1938	Miami	Maracaibo	S.4
	,, ,,	,,		1	,,	,,	Port of Spain	,,
	,, ,,	,,		1	,,	,,	Merida	S.2
68	S. nigra, Macq.	Orig.	5	1	30.10.37	Khartoum	Cairo	E.F.B.
	,, ,,	,,		2	15.5.37	,,	Durban	,,
	,, ,,	,,		1	1.10.37	,,	,,	,,
	,, ,,	,,		1	17.10.37	,,	,,	,,
69	S. taeniata, Bezzi	,,	1		4.10.37	,,	Cairo	,,
70	Glossina pallidipes, Aust.	Symes (*a*)	1			Kisumu		Atalanta
71	Musca alba, Mall.	Orig.	1		1.2.36	Khartoum	Asmara	S-M.
72	M. tempestiva, Fln.	,,	1		12.10.36	,,	,,	,,

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

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No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Diptera—*Cont.* MUSCIDAE—*Cont.*							
73	M. sorbens v. alba, Mall.	Orig.	6	1	5.7.38	Khartoum	Durban	E.F.B.
	,, ,,	,,		1	9.7.38	,,	,,	,,
	,, ,,	,,		1	15.7.38	,,	,,	,,
	,, ,,	,,		1	6.8.38	,,	,,	,,
	,, ,,	,,		1	30.8.38	,,	,,	,,
	,, ,,	,,		1	28.8.38	,,	Asmara	S-M.
74	M. sorbens, Wied.	,,	850+		July 1935 to Aug. 1938	,, ,,	From all parts but most from Asmara, and then the South	All types of planes
75	M. domestica, L.	,,	550+		,,	,,	,, ,,	,,
	,, ,,	Welch	169		1938	Miami	All parts	,,
76	M. domestica vicina, Macq.	Orig.	25	1	9.7.38	Khartoum	Durban	E.F.B.
	,, ,, ,,	,,		3	5.7.38	,,	,,	,,
	,, ,, ,,	,,		10	24.7.38	,,	Asmara	S-M.
	,, ,, ,,	,,		1	28.8.38	,,	,,	,,
	,, ,, ,,	,,		2	3.8.38	,,	,,	,,
	,, ,, ,,	,,		3	6.8.38	,,	,,	,,
	,, ,, ,,	,,		1	16.8.38	,,	,,	,,
	,, ,, ,,	,,		4	27.8.38	,,	,,	,,
77	Muscina stabulans, Fall.	,,	2		23.7.37	,,	Durban	E.F.B.
	Unidentified Muscidae	Symes	15		1934	Kisumu	North	H.P.H. ?
	,, ,,	,,	11		,,	,,	South	,,
	" Flies "	Ross (*a*)	191+		1938	Durban	North	E.F.B.
	ANTHOMYIIDAE							
78	Lispa pygmaea, Fall.	Orig.	7	4	26.7.37	Khartoum	Tripoli	S-M.
	,, ,, ,,	,,		1	29.7.37	,,	Cairo	E.F.B.
	,, ,, ,,	,,		1	23.8.37	,,	,,	,,
	,, ,, ,,	,,		1	15.7.37	,,	Lagos	D.H.86
79	Fannia canicularis, L.	,,	1		9.7.38	,,	Durban	E.F.B.
80	Fannia sp.	,,	3		12.9.36	,,	Lagos	D.H.86
	BORBORIDAE							
81	Leptocera sp.	Welch	1		1938	Miami	Maracaibo	S.4
	LONCHAEIDAE							
82	Lonchaea aurea, Macq.	Orig.	2	1	2.6.36	Khartoum	Capetown	H.P.H.
	,, ,, ,,	,,		1	4.3.37	,,	Asmara	S-M.
	TRYPETIDAE							
83	Acrosticta apicalis, Will.	Welch	4	1	1938	Miami	Barranquilla	S.4
	,, ,, ,,	,,		3	,,	,,	Rio de Janeiro	,,
84	Acrosticta sp.	,,	3		,,	,,	Barranquilla	,,
85	Euxesta notata, Wied.	,,	2	1	,,	,,	,,	,,
	,, ,, ,,	,,		1	,,	,,	Port of Spain	,,
86	Euxesta quaternaria (?)	,,	1		,,	,,	Barranquilla	,,
87	Euxesta sp.	,,	1		,,	,,	San Juan	S.2
	SEPSIDAE							
88	Piophila casei, L.	,,	1		,,	,,	Merida	,,
	ORTALIDAE							
89	Chrysomyza demandata, F.	Orig.	4	1	19.4.37	Khartoum	Cairo	H.P.H.
	,, ,,	,,		2	26.10.37	,,	Tripoli	S-M.
	,, ,,	,,		1	26.5.36	,,	Capetown	H.P.H.

TABLE X—*Continued.*

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No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Diptera—*Cont.*							
	CHLOROPIDAE							
90	Hippelates pallipes, Lw. ...	Welch	3		1938	Miami ...	Port of Spain ...	S.4
91	Hippelates sp.	,,	3	1	,,	,, ...	Barranquilla ...	,,
	,, ...	,,		1	,,	,, ...	Cristobal ...	,,
	,, ...	,,		1	,,	,, ...	Maracaibo ...	,,
92	Prohippelates pallidus, Lw.	,,	2		,,	,, ...	Cristobal ...	,,
93	Oscinella sp.	,,	1		,,	,, ...	Maracaibo ...	,,
	EPHYDRIDAE							
94	Scatella sp.	,,	4	3	,,	,, ...	Barranquilla ...	,,
	,, ...	,,		1	,,	,, ...	Port of Spain ...	,,
95	Plagiops sp.	,,	1		,,	,, ...	Buenos Aires ...	,,
	DROSOPHILIDAE							
96	Gitonides debilis, Walk. ...	Orig.	9	1	14.7.35	Khartoum ...	Cairo ...	H.P.H.
	,, ,, ,, ...	,,		1	28.7.35	,, ...	,, ...	,,
	,, ,, ,, ...	,,		5	3.8.35	,, ...	Capetown ...	,,
	,, ,, ,, ...	,,		1	6.8.35	,, ...	,, ...	,,
	,, ,, ,, ...	,,		1	10.8.35	,, ...	Asmara ...	S-M.
97	G. perspicax, Knab ...	,,	1		23.6.37	,, ...	Lagos ...	D.H.86
98	Drosophila melanogaster, Mg.	Welch	7	2	1938	Miami ...	Barranquilla ...	S.4.
	,, ,,	,,		3	,,	,, ...	Rio de Janeiro	,,
	,, ,,	,,		1	,,	,, ...	Buenos Aires ...	,,
	,, ,,	,,		1	,,	,, ...	Port of Spain ...	,,
99	D. melanica (?) ., ...	,,	1		,,	,, ...	Cristobal ...	,,
100	D. repleta, Woll. ...	,,	5	3	,,	,, ...	Barranquilla ...	,,
	,, ,, ...	,,		1	,,	,, ...	Merida ...	S.2
	,, ,, ...	,,		1	,,	,, ...	Buenos Aires ...	S.4
101	Drosophila sp. ...	,,	3	2	,,	,, ...	Cristobal ...	,,
	,, ,, ...	,,		1	,,	,, ...	Buenos Aires ...	,,
	Unidentified Drosophilidae	Orig.	3	1	10.10.36	Khartoum ...	Asmara ...	S-M.
	,, ,,	,,		1	12.10.36	,, ...	,, ...	,,
	,, ,,	,,		1	29.1.37	,, ...	,, ...	,,
	MILICHIDAE							
102	Desmometopa m-nigrum, Zett	,,	1		6.8.35	,, ...	Capetown ...	H.P.H.
103	Desmometopa sp. n. ? ...	,,	1		19.7.38	,, ...	Durban ...	E.F.B.
	AGROMYZIDAE							
104	Agromyza sp.	Welch	1		1938	Miami ...	Port of Spain ...	S.4
	Unidentified Agromyzidae	,,	1		,,	,, ...	,, ...	,,
	HIPPOBOSCIDAE							
105	Hippobosca maculata, Leach	Orig.	3	1	18.8.36	Khartoum ...	Capetown ...	H.P.H.
	,, ,, ,,	,,		1	24.7.35	,, ...	Asmara ...	S-M.
	,, ,, ,,	,,		1	12.2.37	,, ...	,, ...	,,
106	H. camelina, Leach ...	,,	1		2.1.37	,, ...	,, ...	,,
	Unidentified Hippoboscidae	,,	1		29.8.36	,, ...	,, ...	,,
	Unidentified Diptera ...	Symes	8		1934	Kisumu ...	North ...	H.P.H. ?
	,, ,, ...	,,	16		,,	,, ...	South ...	,,
	,, ,, ...	,,	2		8-12.33-34	Nairobi ...	,, ...	,,
	,, "Hippo" flies	Ross & (*a*)	22+		1937–8	Durban ...	North ...	E.F.B.
	,, "Lake" flies	,,	163+		,,	,, ...	,, ...	,,
	,, "Gnats" ...	,,	16+		,,	,, ...	,, ...	,,
	Very small flies	,,	92+		,,	,, ...	,, ...	,,
	"Fruit" flies	,,	2		,,	,, ...	,, ...	,,

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus †.

No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Diptera—*Cont.*							
	Unidentified Diptera ...	Welch	6	2	1938	Miami ...	Cristobal ...	S.4.
	,, ,, ...	,,		3	,,	,, ...	Rio de Janeiro	,,
	,, ,, ...	,,		1	,,	,, ...	Port of Spain ...	,,
	,, ,, ...	Orig.**	32		1935-1938	Khartoum ...	All parts ...	All types
	APHANIPTERA							
107	Unidentified	Orig.	1		9.36	,, ...	Capetown ...	H.P.H.
	Coleoptera							
	CARABIDAE							
108	Bembidion sp.	Welch	1		1938	Miami ...	Cristobal ...	S.4
	NITIDULIDAE							
109	Cryptarcha sp.	Orig.	1		6.8.35	Khartoum ...	Cairo ...	H.P.H.
	COCCINELLIDAE							
110	Ortalia pallens, Muls. ...	,,	1		28.9.35	,, ...	Cape Town ...	,,
111	Stictoleis pardalina, Gerst. var.	,,	1		3.9.35	,, ...	,, ...	,,
112	Coccinella 11-punctata, L.	,,	14	3	5.4.36	,, ...	Cairo ...	,,
	,, ,, ...	,,		1	26.9.36	,, ...	,, ...	,,
	,, ,, ...	,,		1	18.3.37	,, ...	Tripoli ...	S-M.
	,, ,, ...	,,		1	20.3.37	,, ...	Cairo ...	H.P.H.
	,, ,, ...	,,		1	25.3.37	,, ...	,, ...	,,
	,, ,, ...	,,		1	27.4.37	,, ...	Tripoli ...	S-M.
	,, ,, ...	,,		2	28.3.38	,, ...	Cairo ...	E.F.B.
	,, ,, ...	,,		1	4.4.38	,, ...	,, ...	,,
	,, ,, ...	,,		1	15.8.36	,, ...	Asmara ...	S-M.
	,, ,, ...	,,		2	24.7.38	,, ...	,, ...	,,
113	Adonia variegata tredecim-signata, Muls.	,,	2	1	28.12.37	,, ...	,, ...	,,
	,, ,, ,,	,,		1	28.7.38	,, ...	Durban ...	E.F.B.
114	Scymnus sp.	,,	1		13.8.35	,, ...	Capetown ...	H.P.H.
115	Cycloneda sanguinea, L. ...	Welch	2	1	1938	Miami ...	Cristobal ...	S.4
	,, ,, ...	,,		1	,,	,, ...	Merida ...	S.2
	DERMESTIDAE.							
116	Phradonoma nobile, Rtt. ...	Orig.	1		5.10.36	Khartoum ...	Asmara ...	S-M.
117	Attagenus sp.	Welch	1		1938	Miami ...	Maracaibo ...	S.4
	BOSTRYCHIDAE							
118	Sinoxylon ruficorne, Fhs. ...	Orig.	2	1	5.10.36	Khartoum ...	Cairo ...	H.P.H.
	,, ,, ,, ...	,,		1	27.4.37	,, ...	Lagos ...	D.H.86
119	Xylopsocus sellatus, Fhs. ...	,,	1		2.2.37	,, ...	Capetown ...	H.P.H.
	MELYRIDAE							
120	Hedybius luteus, Roth. ...	,,	1		6.8.36	,, ...	Asmara ...	S-M.
	TELEPHORIDAE							
121	Chauliognathus marginatus, F.	Welch	1		1938	Miami ...	Cristobal ...	S.4

** See end of Table.

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

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No. of spp.	Insect	Author	No. of insects	Date	Where collected	Plane from	Type of plane
	Coleoptera—*Cont.*						
	ELATERIDAE						
122	Cardiophorus sp.	Orig.	1	14.11.36	Khartoum ...	Capetown ...	H.P.H.
	BUPRESTIDAE						
123	Agrilus fryi, Obenb. ...	,,	1	4.9.37	,, ...	Asmara ...	S-M.
	TENEBRIONIDAE						
124	Anemia thoracica, Frm. ...	,,	1	22.9.36	,, ...	Capetown ...	H.P.H.
125	Opatrinus niloticus, Muls.	,,	1	14.11.36	,, ...	,, ...	,,
	MELOIDAE						
126	Mylabris nubica, Boh. ...	,,	2	28.7.38	,, ...	Durban ...	E.F.B.
	APHODIIDAE						
127	Aphodius marginellus, F....	,,	1	2.2.37	,, ...	Capetown ...	H.P.H.
	MELOLONTHIDAE						
128	Triodonta sp.	,,	1	15.8.36	,, ...	,, ...	,,
	RUTELIDAE						
129	Adoretus clypeatus, Burm.	,,	2	5.10.35	,, ...	,, ...	,,
130	Anomala praetendinosa, Ohs.	,,	1	4.4.36	,, ...	,, ...	,,
	DYNASTIDAE						
131	Cyclocephala lunulata, Burm.	Welch	1	1938	Miami ...	Buenos Aires ...	S.4
	PLATYPIDAE						
132	Platypus sp.	Orig.	1	14.11.36	Khartoum ...	Capetown ...	H.P.H.
	BRUCHIDAE						
133	Pachymerus pallidus, Ol. ...	,,	1	20.11.35	,, ...	Tripoli ...	S-M.
	CRIOCERIDAE						
134	Lema melanopa, L. ...	,,	1	22.7.38	,, ...	Durban ...	E.F.B.
	EUMOLPIDAE						
135	Pseudocolaspis sp. ...	,,	1	7.10.35	,, ...	Asmara ...	S-M.
	HALTICIDAE						
136	Podagrica puncticollis, Wse.	,,	1	27.7.35	,, ...	Capetown ...	H.P.H.
	GALERUCIDAE						
137	Monolepta sp.	,,	1	18.9.36	,, ...	Cairo ...	,,
	CASSIDIDAE						
138	Aspidomorpha areata, Kl. var. nigripennis, Wse. ...	,,	1	24.8.35	,, ...	Capetown ...	,,
	Unidentified Coleoptera ...	Welch	3	1938	Miami ...	Port of Spain ...	S.4
	Telanus ? sp.	,,	1	,,	,, ...	Barranquilla ...	,,
	Unidentified Coleoptera ...	Symes	3	1934	Kisumu ...	North ...	H.P.H. ?
	,, ,, ...	,,	2	,,	,, ...	South ...	,,
	,, ,, ...	Orig.**	12	1935-1938	Khartoum ...	All parts ...	All types

** See end of Table.

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus †.

No. of spp.	Insect	Author	No. of insects	Date	Where collected	Plane from	Type of plane
	Hymenoptera						
	Apidae						
139	Megachile gratiosa, Grst.	Orig.	1	27.4.37	Khartoum	Capetown	H P.H.
140	Nomia sp.	,,	1	18.9.36	,,	Tripoli	S-M.
141	Bee (solitary)	Symes	1	8-12.33-34	Nairobi	North	H.P.H. ?
	Sphegidae						
142	Sceliphron quartinae, Grib.	Orig.	1	26.9.36	Khartoum	Asmara	S-M.
143	S. spirifex, L.	,,	1	26.11.37	,,	Durban	E.F.B.
144	Crabro sp.	,,	1	14.11.36	,,	Capetown	H.P.H.
	Scoliidae						
145	Tiphia sp.	Welch	1	1938	Miami	Port of Spain	S.4
146	Myzine sp.	Orig.	1	4.4.36	Khartoum	Capetown	H.P.H.
147	,,	,,	1	12.8.37	,,	Cairo	E.F.B.
148	,,	,,	1	23.7.35	,,	Asmara	S-M.
	Mutillidae						
149	? damaged specimen	,,	1	20.11.35	,,	Cairo	H.P.H.
	Eumenidae						
150	Odynerus sp.	,,	1	20.2.36	,,	Capetown	,,
151	,,	,,	1	1.6.37	,,	Lagos	D.H.86
	Vespidae						
152	Polybia occidentalis, Oliv.	Welch	1	1938	Miami	Barranquilla	S.4
153	Hornet	Symes	1	1934	Kisumu	North	H.P.H. ?
	Chrysididae						
154	Chrysis stilboides, Spin.	Orig.	1	18.8.36	Khartoum	Asmara	S-M.
155	C. nigeriaca, Mocs.	,,	1	9.7.37	,,	Lagos	D.H.86
156	Chrysis sp.	,,	1	7.10.35	,,	Asmara	S-M.
	Formicidae						
157	Tanaemyrmex maculatus, F.	,,	2	5.7.37	,,	Cairo	E.F.B.
158	Camponotus sericeus, F.	,,	1	28.7.38	,,	Durban	,,
159	Prenolepis longicornis, Latr., worker	Welch	4	1938	Miami	Barranquilla	S.4
160	Tetramorium guineense, F., worker	,,	1	,,	,,	Buenos Aires	,,
161	Ponera sp.	,,	1	,,	,,	Barranquilla	,,
162	Pheidole sp.	,,	1	,,	,,	Buenos Aires	,,
163	Tribe Attini	,,	1	,,	,,	Port of Spain	,,
	Unidentified Formicidae	Orig.	1	1.5.37	Khartoum	Capetown	H.P.H.
	" Flying ants "	Ross (*a*)	4	1938	Durban	North	E.F.B.
	Chalcididae						
164	Brachymeria sp.	Orig.	1	28.12.37	Khartoum	Asmara	S-M.
165	B. amenocles, Wlk.	,,	1	28.7.38	,,	Durban	E.F.B.
	Evaniidae						
166	Evania dimidiata, F.	,,	1	10.10.36	,,	Lagos	D.H.86
	Ichneumonidae						
167	Osprynchotus flavipes, Brullé	,,	1	7.8.38	,,	Durban	E.F.B.
168	Tribe Campoplegini	,,	1	10.10.36	,,	Asmara	S-M.
	Unidentified Ichneumonidae	Symes	4	1934	Kisumu	South	H.P.H. ?

TABLE X.—*Continued.*

Insects found in Commercial Aircraft—World List.

Insects proved to have transmitted yellow fever by bite under laboratory conditions shown thus *. Insects proved to retain the virus in their bodies shown thus †.

No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Hymenoptera—*Cont.*							
	BRACONIDAE							
169	Phanerotoma hendecasiella, Cam.	Orig.	1		20.11.35	Khartoum ...	Cairo	H.P.H.
170	Phanerotoma sp.	,,	1		16.7.38	,, ...	Durban ...	E.F.B.
171	Disophrys lutea, Brullé ...	,,	1		18.8.36	,, ...	Asmara ...	S-M.
172	Apanteles sp.	Welch	1		1938	Miami ...	Barranquilla ...	S.4
	Unidentified Hymenoptera	Ross (*a*)	1		,,	Durban ...	North	E.F.B.
	,, ,, ...	Symes	3		1934	Kisumu ...	South	H.P.H.
	,, ,, ...	Orig.**	15		1935–1938	Khartoum ...	All parts ...	All type
	Lepidoptera							
	AGARISTIDAE							
173	Aegocera rectilinea, Boisd.	Orig.	1		27.4.37	Khartoum ...	Lagos	D.H.86
174	Cydosia nobilitella, Cram....	Welch	1		1938	Miami ...	Port of Spain ...	S.4
	NOCTUIDAE							
175	Sphingomorpha chlorea, Cram.	Orig.	4		31.3.36	Khartoum ...	Capetown ...	H.P.H.
176	Perigea illecta, Wlk. ...	,,	1		22.9.36	,, ...	,, ...	,,
177	Eublemma gayneri, Roths.	,,	1		28.7.38	,, ...	Durban ...	E.F.B.
178	Agrotis ypsilon, Hb. ...	,,	1		30.9.37	,, ...	Cairo	,,
179	Grammodes stolida, F. ...	,,	1		28.9.35	,, ...	Capetown ...	H.P.H.
180	Laphygma frugiperda, S. & A.	Welch	2	1	1938	Miami ...	Barranquilla ...	S.4
	,, ,, ,, ,,	,,		1	,,	,, ...	Cristobal ...	,,
	SPHINGIDAE							
181	Hippotion celerio, L. ...	Orig.	1		20.2.36	Khartoum ...	Capetown ...	H.P.H.
	GEOMETRIDAE							
182	Omphacodes divergens, Warr.	,,	1		12.9.36	,, ...	,, ...	,,
	PSYCHIDAE							
183	Acrolophus sp. ...	Welch	1		1938	Miami ...	Barranquilla ...	S.4
	PYRALIDAE							
184	Pyrausta sp.	,,	1		1938	,, ...	Rio de Janeiro	,,
185	Nomophila noctuella, Schiff.	Orig.	1		30.7.36	Khartoum ...	Cairo	H.P.H.
186	Ommatopteryx ocellea, Haw.	,,	3	1	13.2.37	,, ...	,, ...	,,
	,, ,, ,,	,,		2	15.2.37	,, ...	Tripoli ...	S-M
187	Achroia ? grisella, F. ...	,,	1		27.4.37	,, ...	Capetown ...	H.P.H.
188	Ephestia sp.	,,	1		18.8.36	,, ...	,, ...	,,
189	,, ,, ...	,,	1		22.9.37	,, ...	Durban ...	E.F.B.
190	Elasmopalpus lignosellus, Zell.	Welch	2		1938	Miami ...	Barranquilla ...	S.4
191	Hellula phidilealis, Walk....	,,	1		,,	,, ...	Maracaibo ...	,,
192	Plodia interpunctella, Hb.	,,	1		,,	,, ...	Merida ...	S.2
	PTEROPHORIDAE							
193	Agdistis sp.	Orig.	1		11.2.37	Khartoum ...	Asmara ...	S-M.
	Undeterminable Pterophoridae	,,	2		5.10.36	,, ...	Cairo	H.P.H.
	TINEIDAE							
194	Plutella maculipennis, Curt.	,,	1		20.7.36	,, ...	,, ...	,,

** See end of Table.

TABLE X—*Continued.*

Insects found in Commercial Aircraft—World List.

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No. of spp.	Insect	Author	No. of insects		Date	Where collected	Plane from	Type of plane
	Lepidoptera—*Cont.*							
	GELECHIIDAE							
195	Dichomeris rustica, Wals.	Welch	1		1938	Miami	Merida	S.2
196	Recurvaria sp.	,,	1		,,	,,	,,	,,
	Unidentified Gelechiidae	Orig.	1		12.10.36	Khartoum	Asmara	S-M.
	Unidentified Lepidoptera	Welch	2	1	1938	Miami	Port of Spain	S.4
	,, ,,	,,		1	,,	,,	Merida	S.2
	,, ,, (moths)	Symes	10		1934	Kisumu	South	H.P.H.
	,, ,, (moths)	Ross & (*a*)	14		1937-8	Durban	North	E.F.B.
	,, ,,	Orig.**	17		1935-1938	Khartoum	All parts	All types
	Orthoptera							
	BLATTIDAE							
197	Supella sp.	Welch	1		1938	Miami	Rio de Janeiro	S.4
198	S. supelectilium, Serv. adult (♀ laying eggs)	Orig.	2	1	22.3.38	Khartoum	Asmara	S-M.
	,, ,, ,,	,,		1	9.7.38	,,	Durban	E.F.B.
	,, ,, larvae	,,	4	1	16.12.35	,,	Cairo	H.P.H.
	,, ,, ,,	,,		1	27.7.35	,,	Capetown	,,
	,, ,, ,,	,,		1	24.12.35	,,	,,	,,
	,, ,, ,,	,,		1	29.12.35	,,	,,	,,
199	Blatella germanica, L.† adult	,,	5	2	30.5.36	,,	,,	,,
	,, ,, ,,	,,		1	2.6.36	,,	,,	,,
	,, ,, ,,	,,		2	9.1.37	,,	Cairo	,,
	,, ,, larva	,,	1		2.6.36	,,	Capetown	,,
200	Blatella sp.	,,	1		16.7.38	,,	Durban	E.F.B.
201	Periplaneta australasiae, F.	Welch	1		1938	Miami	Maracaibo	S.4
	Unidentified Blattidae (larva)	Orig.	1		17.9.35	Khartoum	Capetown	H.P.H.
	,, ,,	Welch	9	2	1938	Miami	Barranquilla	S.4
	,, ,,	,,		6	,,	,,	Cristobal	,,
	,, ,,	,,		1	,,	,,	Port of Spain	,,
	,, ,,	Symes	1		1934	Kisumu	North	H.P.H.
	,, ,, (larva)	,,	1		,,	,,	South	,,
	Living in wings of planes	Michel	many					
	GRYLLIDAE							
202	Gryllus bimaculatus, De G.	Orig.	1		5.11.35	Khartoum	Capetown	H.P.H.
203	G. domesticus, L.	,,	1		18.8.36	,,	Asmara	S-M.
204	Gryllodes sigillatus, Wlk.	,,	1		1.5.37	,,	Capetown	H.P.H.
	Unidentified Gryllidae	Welch	1		1938	Miami	Rio de Janeiro	S.4
	TETTIGONIIDAE							
205	Pseudorhynchus werneri, Karny	Orig.	1		27.4.37	Khartoum	Capetown	H.P.H.
	ACRIDIDAE							
206	Pyrgomorpha cognata, Kr.	,,	1		28.7.35	Khartoum	Cairo	H.P.H.
207	Cantatops saucius, Burm.	,,	1		19.3.36	,,	,,	,,
208	Anacridium moestum melanorhodon, Wlk.	,,	1		14.11.36	,,	Capetown	,,
	Unidentified Orthoptera	Symes	2		1934	Kisumu	South	H.P.H.?
	,, ,,	Ross	few		1937	Durban	North	E.F.B.
	,, ,,	Orig.**	4		30.5.36–23.8.36	Khartoum	All parts	All types

** See end of Table.

TABLE X—*Continued.*

Insects found in Commercial Aircraft—World List.

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No. of spp.	Insect	Author	No of insects	Date	Where collected	Plane from	Type of plane
	Hemiptera CYDNIDAE						
209	Larva ?	Orig.	1	3.9.35	Khartoum ...	Cairo	H.P.H.
	COREIDAE						
210	Liorhyssus hyalinus, F. ...	,,	1	22.9.36	,, ...	Capetown ...	,,
	BERYTIDAE						
211	Capyella sp.	,,	1				
	LYGAEIDAE						
212	Nysius sp.	,,	3	4.8.36	,, ...	Capetown ...	,,
213	Lygaeus pandurus, Scop. ...	,,	1	27.4.37	,, ...	Cairo	,,
214	Lygaeus sp.	Welch	1	1938	Miami ...	Barranquilla ...	S.4
	CIMICIDAE						
215	Cimex hemipterus, F.† ...	Orig.	1	26.9.36	Khartoum ...	Asmara ...	S-M.
	CAPSIDAE						
216	Sixeonotus sp.	Welch	1	1938	Miami ...	Rio de Janeiro	S.4
	JASSIDAE						
217	Thamnotettix sp.	Orig.	1	19.9.36	Khartoum ...	Lagos ...	D.H.86
218	Athysanus sp.	,,	1	14.11.36	,, ...	Capetown ...	H.P.H.
	Unidentified Hemiptera ...	,, **	7	1935-1938	,, ...	All parts ...	All types
	Neuroptera CHRYSOPIDAE						
219	Chrysopa sp.	Orig.	1	14.1.36	,, ...	Capetown ...	H.P.H.
	EPHEMERIDAE						
220	Aphroneurus sp.	,,	1	19.9.36	,, ...	,, ...	,,
221	Cloeon sp.	,,	3 1	26.9.36	,, ...	Asmara ...	S-M.
	,, ,, ...	,,	1	15.12.37	,, ...	Cairo ...	E.F.B.
	,, ,, ...	,,	1	10.7.38	,, ...	Durban ...	,,
	Unidentified Ephemeridae	Symes	1	1934	Kisumu ...	South ...	H.P.H.
	Odonata						
222	Dragon fly	Ross (*a*)	1	1938	Durban ...	North ...	E.F.B.
	Dermaptera FORFICULIDAE						
223	Forficula senegalensis, Serv.	Orig.	1	1.6.37	Khartoum ...	Lagos	D.H.86
	Trichoptera POLYCENTROPIDAE						
224	Dipseudopsis capensis, Walk.	,,	1	27.4.37	,, ...	Capetown ...	H.P.H.
225	Dipseudopsis sp.	,,	2	19.7.38	,, ...	Durban ...	E.F.B.
	Araneida						
226	Plexeppus sp.	Welch	1	1938	Miami ...	Barranquilla ...	S.4
227	Dendryphantes sp. ...	,,	1	,,	,, ...	Buenos Aires ...	,,

** Some of the insects marked thus were specimens found by the writer on his return from leave in August 1936 (see p. 403) in too bad condition for other than ordinal determination. The remainder had been damaged in the planes.

Identifications.—All Khartoum insects were examined by the writer, roughly identified, and then sent to the Imperial Institute of Entomology (see " Acknowledgments ").

Discussion of Data in Table X.

Geographical Synopsis of the Insect Records in Table X.

AFRICA. Khartoum. Insects recorded in :—

Planes from the North (H.P.H., E.F.B. and S.M.) those from Tripoli only, marked thus * ; those from Tripoli as well as Cairo marked thus †.—Nos. 3, 7, 18, ~~21~~, 32, 57, 63, 67, 68, 69, 74, 75, 78†, 89†, 96, 109, 112†, 118, 133*, 137, 140*, 147, 149, 157, 169, 178, 185, 186†, 194, 198, 199, 206, 207, 209, 213, 221. Total 36, and unidentified Anopheles, Culicines† and Pterophoridae. 5 +

Planes from the South (H.P.H. and E.F.B.).—Nos. 7, 8, 11, 12, 13, 14, 24, 25, 26, 31, 33, 42, 43, 44, 45, 46, 63, 66, 67, 68, 73, 74, 75, 76, 77, 79, 82, 89, 96, 102, 103, 105, 107, 110, 111, 113, 114, 119, 122, 124, 125, 126, 127, 128, 129, 130, 132, 134, 136, 138, 139, 143, 144, 146, 150, 158, 165, 167, 170, 175, 176, 177, 179, 181, 182, 187, 188, 189, 198, 199, 200, 202, 204, 205, 208, 210, 212, 218, 219, 220, 221, 224, 225. Total 83, and unidentified Culicines, Formicidae and Blattidae.

Planes from the East (S-M.).—Nos. 7, 17, 19, 22, 23, 33, 34, 35, 58, 59, 60, 61, 66, 67, 71, 72, 73, 74, 75, 76, 82, 96, 105, 106, 112, 113, 116, 120, 123, 135, 142, 148, 154, 156, 164, 168, 171, 193, ~~195~~, 198, 203, 215, 221. Total 43, and unidentified Anopheles, Culicines, Drosophilidae, Hippoboscidae and Gelechiidae. 62,

Planes from the West (D.H. 86).—Nos. 17, 47, 56, 67, 74, 75, 78, 80, 97, 118, 151, 155, 166, 173, 217, 223. Total 16.

Kisumu. North (H.P.H. and Atalantas).—Nos. 11, 12, 153, and unidentified Chironomidae, Culicines, Tabanidae, Muscidae, Diptera, Coleoptera and Blattidae. South.—Nos. 7, and unidentified Culicines, Muscidae, Diptera, Coleoptera, Ichneumonidae, Hymenoptera, Lepidoptera, Blattidae, Orthoptera and Ephemeridae. ? No. 70.

Nairobi. North (H.P.H. and Atalantas).—11, 12, 141. Unidentified Culicines. South.—11. Unidentified Chironomidae, Culicines and Diptera.

Durban, North (E.F.B.).—222. Unidentified Chironomidae, Anopheles, Aëdes, Culicines, Culicidae, Tabanidae, Muscidae, Diptera, Formicidae, Hymenoptera, Lepidoptera and Orthoptera.

Coquilhatville.—Unidentified Mansonia.

Leopoldville.—Unidentified Culicines, Mansonia and Aëdes.

CENTRAL AND SOUTH AMERICA.—Miami. Insects recorded in planes from :—

Merida (S.2).—Nos. 48, 55, 67, 75, 88, 100, 115, 192, 195, 196. Total 10. Unidentified Lepidoptera.

Cristobal (S.4).—Nos. 5, 27, 41, 49, 64, 75, 91, 92, 99, 101, 108, 115, 121, 180. Total 14. Unidentified Diptera and Blattidae.

Barranquilla (S.4.).—Nos. 1, 2, 5, 20, 21, 27, 32, 40, 50, 51, 52, 53, 54, 55, 65, 75, 83, 84, 85, 86, 91, 94, 98, 100, 152, 159, 161, 172, 180, 183, 190, 214, 226. Total 33, and unidentified Culicidae, Culicines, Coleoptera and Blattidae.

Maracaibo (S.4).—Nos. 6, 7, 9, 10, 15, 27, 39, 53, 67, 75, 81, 91, 93, 117, 191, 201. Total 16.

San Juan (S.2).—Nos. 1, 7, 27, 32, 55, 75, 87. Total 7. Unidentified Culicines.

Port of Spain (S.4).—Nos. 1, 4, 5, 27, 32, 67, 75, 85, 90, 94, 98, 104, 145, 163, 174, Total 15, and unidentified Mansonia, Agromyzidae, Diptera, Coleoptera, Lepidoptera and Blattidae.

Rio de Janeiro (S.4).—Nos. 1, 32, 75, 83, 98, 184, 197, 216. Total 8, and unidentified Culicines, Diptera and Gryllidae.

Buenos Aires (S.4).—Nos. 75, 95, 98, 100, 101, 131, 160, 162, 227. Total 9.

CENTRAL AND SOUTH AMERICA AND WEST INDIES.

Nos. 15, 16, 20, 21, 27, 30, 32, 36, 37, 38. Total 10, and unidentified Culicidae.

The Khartoum Figures.

Over 2,000 aircraft were examined in the period July 1935–August 1938. Including unidentified specimens 1,960* insects were collected, comprising 146 species. If all specimens of *Musca domestica* and *M. sorbens* be included,† a total of nearly 3,000 insects were collected. The great majority of aircraft examined contained insects; but excluding *Musca* spp., 192 planes contained insects. The following table shows the distribution of planes containing insects other than *Musca* throughout the period under review. The number of planes arriving at Khartoum per week was higher during the latter part of 1937 and 1938 than previously.

TABLE XI.

	1935	1936	1937	1938	Total	Average
January	—	3	4	2	9	3·0
February	—	7	6	1	14	4·66
March	—	3	6	3	12	4·0
April	—	3	6	1	10	3·33
May	—	4	3	0	7	2·33
June	—	2	2	0	4	1·33
July	—	5	8	10	23	7·66
August	10	13	6	9	38	9·5
September	5	16	6	—	27	9·0
October	3	7	10	—	20	6·66
November	3	3	9	—	15	5·0
December	3	0	10	—	13	4·33
Totals	24	66	76	26	192	Average of above 5·07

The average figure obtained from the total number (192) divided by the number of months is 5·18.

The only deduction to be made from the above figures is that insects carried in aircraft, not including *Musca*, are fairly evenly spread throughout the year, with a slight increase during the period June–October. The type of aircraft (*cf.* p. 405) would seem to have little effect upon the figures.

General Nature of the Collections from Aircraft.

Table XII represents an analysis of all insects collected from aircraft, distinguishable as separate species (see p. 405).

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* Including 850 *Musca sorbens* and 550 *M. domestica*.

† The figures 850 for *Musca sorbens* and 550 for *M. domestica* include only those that were actually identified. There were large numbers of Muscidae(?) too damaged for accurate identification.

TABLE XII.

Identified Insects.

Order	Families			Genera			Species			Total No. of Insects including unidentified species			Total of all Countries			
	Sudan	South America	Rest of Africa	Sudan	South America	Rest of Africa	Sudan	South America	Rest of Africa	Sudan	South America	Rest of Africa	Families	Genera	Species	All insects including unidentified
Diptera	14	20	4	29	39	7	56	51	6	*1960 ‖	†717+	‡799+	29	58	106	3476+§‖
Coleoptera	19	5	0	26	5	0	26	5	0	55	10	5	22	31	31	70
Hymenoptera	11	4	4	16	8	4	24	8	—	41	11	14	12	29	34	66
Lepidoptera	8	5	0	14	9	0	15	9	0	40	13	24	9	23	24	77
Orthoptera	4	2	1	8	3	1	10	3	—	25	12	4+	4	9	12	41+
Hemiptera	6	2	0	8	2	0	8	2	0	17	2	0	7	9	10	19
Neuroptera	2	0	1	3	0	1	3	0	—	5	0	1	2	3	3	6
Odonata	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1	1
Dermaptera	1	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1
Trichoptera	1	0	0	2	0	0	2	0	0	3	0	0	1	2	2	3
Aphaniptera	1	0	0	1	0	0	1	0	0	1	0	0	1	1	1	1
Totals	67	38	11	108	66	14	146	78	7	2148	765+	848+	89	167	225	3761+

* Including 850 *Musca sorbens* and 550 *M. domestica.*
† Including 169 *M. domestica* and 300 *Chironomus* sp.
‡ Including large numbers of " Lake flies," " very small flies," " hippo flies," etc.
§ Including all the above.
‖ Excluding large numbers of Diptera debris taken at Khartoum which were too damaged for identification.

A comparison of insects collected from aircraft with those in Tables V and IX*, classified under families, may be expressed as follows :—

TABLE XIII.

No. of families in Table X		No. of families common to Tables X and V (Terrestrial Zone)	No. of families common to Tables X and IX (Plankton Zone)
Diptera	29	24 including large and strong-flying types	12, with the exceptions of Muscidae and Bibionidae all small to minute flies
Coleoptera	22	9 including large and strong-flying types	1
Hymenoptera	12	5 including large and strong-flying types	3 Hymenoptera Parasitica, small weak-flying types
Lepidoptera	9	7 including large and strong-flying types	1 Tineid
Orthoptera	4	3 mostly strong terrestrial types ...	None in Table IX
Hemiptera	7	4 Heteroptera	1 Jassid. The only family of Homoptera in Table X
Neuroptera	2	Also occur in Table .V	1 at 200–400 ft. in Table IX
Odonata	1	,, ,, ,, ,, ...	None in Table IX
Trichoptera	1	,, ,, ,, ,, ...	1 at 200–400 ft. in Table IX

*The actual families are not given in Table V as they would have made it too long. This comparison is based on the original papers, in some of which (Weiss 1927-28 and Felt & Chamberlain 1935) families and species are given.

It is difficult to escape the conclusion that insects collected in aircraft belong mainly to the terrestrial zone ; reference to Table X will confirm this, as most of the families are represented by a large proportion of strong-flying, heavy or terrestrial types most unlikely to be found in the upper air. The only Order in which families of small " plankton " zone types of insect occur to any extent in Table X is the Diptera. The occurrence in aircraft of such insects does not necessarily mean that they were collected during flight, for they are as common, if not more so, at ground-level. The presence of terrestrial zone types, which are not found in the upper air, is however strong evidence to the contrary. The following further comparison provides additional evidence as to the terrestrial nature of the insects found in aircraft :—

Insects in aircraft not occurring in Table IX	Insects from Table IX not occurring in aircraft
1 Cimex hemipterus 1 flea 5 specimens of Hippoboscidae Orthoptera, including such terrestrial types as Blattidae, adults and nymphs, and Gryllidae Odonata Dermaptera	Homoptera, small types typical of the " plankton " zone (the only Homoptera found in aircraft were Jassids) Psocoptera Collembola Spiders (only 2 were taken in aircraft)

The Psocoptera, Collembola, and spiders, though apterous, are nevertheless essentially " plankton " types. The two former are by no means active runners, and are unlikely to gain access to aircraft from the ground, and by reason of their fragility and lightness they are eminently suited to aerial drift. The spiders, according to Crosby & Bishop (1936), were mostly young animals, presumably floating by means of gossamer.

Percentage of Planes with Insects to total Number examined.

The figures are as follows :—

	Including *Musca* spp.	Excluding *Musca* spp.
Khartoum	Over 70 per cent.	Approx. 10 per cent.
Kisumu	34·8 ,,	
Nairobi	17·09 ,,	
Durban	51·4 ,,	21·6 per cent excluding " flies "
Miami	47·4 ,,	

These figures are given as a matter of interest, and can mean little more than that relatively large numbers of insects are carried by aircraft. So many factors enter into the matter that they are valueless for comparison with each other. In the case of Khartoum the aircraft are cleared of insects at the port of entry into the country ; one must conclude that either the treatment as at present carried out by means of hand " flit " pumps and a pyrethrum base insecticide is extremely inefficient, or that insects invade the aircraft after it has been done, or (what is probably the case) that the treatment only kills some of the insects in the planes, many reviving later, and that others enter after it has been done and while the baggage and passengers are embarked. Night stops also probably influence the number and character of insects entering the planes.

Some of the aircraft examined at Khartoum were " flitted " during flight ; when this occurred it did not seem to have much effect upon the insects found. A large number of the insects collected at Khartoum were alive when caught. In the cases of Durban and Miami the larger proportion of insects collected were dead, owing partly to treatment during flight, but Ross's (1938, unpubl.) figures indicate that many insects die from other causes, and that hand-pump treatment is by no means efficient ; this is borne out by Welch's (1939) and the writer's observations.

It is interesting to note the large proportion of *Musca* spp. in the Khartoum figures, the greater proportion of aircraft with insects (including *Musca*) at Khartoum being possibly due to the methods of search, and the longer time to carry it out in comparison with the methods of other workers.

The nature of the airport and its surroundings must necessarily play a part in the number and type of insects found ; thus the Abyssinian war and conditions resulting therefrom were probably the reason for so many *Musca* and the greater number of mosquitoes found in planes from Asmara as compared with other localities.

Insects appear to show a tendency to remain in aircraft for some time. Griffitts & Griffitts (1931) and Griffitts (1933) have shown that, even with many intermediate stops, stained mosquitoes were still found in the planes on arrival at Miami after a journey of 79 hours. During the three year period of the work in Khartoum, watch was kept at the cabin and baggage doors of all aircraft, and no instance was ever reported of insects escaping while passengers and baggage were disembarked. These results are subject to human fallibility, and it is admittedly difficult to keep such a watch, nevertheless the general implication agrees with the Griffitts' experiments, and the origin of the insects found in aircraft is thus inevitably a matter of conjecture.

This tendency for insects to remain in the planes has been noticed by the writer to be the case also with trains and river steamers, but not with cars. This is only to be expected when the design and construction of the various types of transport are considered. The writer has many times noticed that even in saloon cars insects have a tendency to escape as soon as possible.

The Relation of the Type of Plane to the Carriage of Insects.

There would appear to be little or no relation between the numbers of insects carried by aircraft, and the type of the latter. Four main types of commercial aircraft used Khartoum airport during the three years under review, varying from the obsolete Hannibals and the relatively old-fashioned D.H. 86's to the modern Empire Flying Boats and the Savoia-Marchettis.

Welch's (1939) collections were made from modern Sikorsky Clippers and the Durban results are from the Empire Flying Boats, while Symes' (1935–36–37) were presumably made in the older types.

Insects of Medical Importance found in the Aircraft.

A fairly wide range of Culicidae was taken, as follows: 28 species comprising over 381 specimens composed of over 169 identified and over 212 unidentified specimens distributed as under:—

Africa	Central and South America (Miami)
19 species Identified specimens 94+ Unidentified specimens 204+ belonging to the following genera: *Anopheles* 4 spp. *Theobaldia* 1 sp. *Mansonia* 2 spp. *Aedes* 8 spp. *Culex* 4 spp.	11 species Identified specimens 76+ Unidentified specimens 8 belonging to the following genera: *Anopheles* 2 spp. *Mansonia* 2 spp. *Aëdes* 3 spp. *Culex* 2 spp. *Psorophora* 2 spp.

in addition to which 15 specimens of *Chaoborus* sp. were taken at Miami.

Chronologically there would appear to be little significance in the figures.

The following is a list of the insects associated with yellow fever which have been taken in aircraft:—

Species proved to have transmitted the virus by bite under lab. conditions	Species proved to retain the virus in their bodies
Culex fatigans	*Anopheles gambiae*
Mansonia africana	*Mansonia uniformis*
Aëdes simpsoni	*M. titillans*
A. luteocephalus	*Blatella germanica*
A. taeniorhynchus	*Cimex hemipterus*

The malarial vectors taken in aircraft were:—

Anopheles gambiae ...	Tropical Africa, Sudan, S. Arabia, etc.
A. funestus	,, ,, ,, ,,
A. albimanus	Central America and West Indies.
A. pseudopunctipennis	Argentina (particularly in the hills).
A. pharoensis ...	Egypt.

It is not proposed to discuss in detail the diseases carried by insects, but with regard to insects found in aircraft the facts that various species of *Aëdes*, and perhaps *Culex*, have been associated with the transmission of dengue, and that various

Filariae are known to be carried by mosquitoes, are of significance. The occurrence of a specimen each of *Glossina pallidipes*, *Cimex hemipterus*, and a flea needs no emphasising, while the presence of a number of TABANIDAE brings the possibility of the mechanical transmission of various diseases to the fore. The carriage of large numbers of *Musca* spp. is a matter of obvious concern, and the careful collection of all insects at Khartoum probably prevented infection from Asmara and the Abyssinian area from being disseminated in the town. The occurrence of a specimen of the cheese maggot fly (*Piophila casei*) is of interest.

The occurrence of cockroaches in the wings of aircraft apparently feeding on the glue and dope (Michel, " Sur la destruction des moustiques à bord des aeronefs," 1935) and the finding of adults (one about to lay eggs) and nymphs in Khartoum aircraft is of interest when Findlay & MacCallum's work (1939) is considered.

Insects of Veterinary Importance taken in Aircraft.

Vectors of the following diseases have been found :—

Equine Encephalomyelitis : *Aëdes sollicitans, A. taeniorhynchus, A. aegypti.*
Blue Tongue : *Aëdes lineatopennis.*
African Horse Sickness : *Stomoxys calcitrans.*
Equine Infectious Anaemia : *Stomoxys calcitrans.*
Fowl Pox : *Aëdes aegypti, Culex fatigans, Stomoxys calcitrans.*
(The above are all virus diseases.)
Canine Filariasis : *Aëdes aegypti.*

Insects of Agricultural Importance found in Aircraft.

Apart from the discovery of portions of a dead specimen of *Leucopholis irrorata*, Chevr., in a Philippine " Clipper " from the Orient (Pemberton, 1938), no non-cosmopolitan insect of major economic importance has yet been recorded from aircraft. The possibility of such an occurrence is obvious.

It should be remembered that the list of insects presented in Table X is merely an indication of what is probably continuously occurring. Although insects seem to show a tendency to remain in the aircraft for some time, numbers probably escape at uncontrolled intermediate stops, and if research were continued over a period of years, and at other airports, the list would probably include many more species of medical, veterinary and agricultural importance.

Rats in Aircraft.

Rats have been recorded from time to time, and rat excreta have been noticed in aircraft. The large modern air liner offers excellent hiding places for rats, and with the steady increase in size of commercial aircraft the rat problem will become important.

Control of Insects in Aircraft.

The control of insects in aircraft is a difficult problem which involves the co-operation of the entomologist, the chemist and the engineer, an airline operating company and a commercial aircraft manufacturer. No such joint approach to the problem has, so far as the writer is aware, yet been attempted, but until it is forthcoming little progress can be expected.

Such work as has been done has been concerned for the most part with the destruction of mosquitoes, and beyond the evolution of a non-inflammable pyrethrum-base insecticide, little progress has been made.

The writer, lacking facilities in Khartoum for such research, is unable to offer definite suggestions, but the study of the problem under natural working conditions has led to the following conclusions.

Evidence has been put forward as to the difficulty of keeping airports, and aircraft alighting upon them, free from insects. The fact that no such control has yet been achieved is borne out by the list of insects found in aircraft in different parts of the world. Intermediate and Air Force aerodromes, particularly in wild tropical country, can never be maintained free from insects, and even in Europe airports such as Croydon and Le Bourget are not without them.

Entry of Insects into Aircraft during Flight.

The evidence of Table X with its mainly terrestrial type of insects is corroborated by captains and pilots of aircraft with whom the writer has discussed the question. They have never noticed insects invade their craft while in flight, except under abnormal conditions, such as the encounter of flights of locusts, or clouds of " lake " flies (Chironomids) etc.*

The older types of air liner might conceivably have offered external shelter to insects, even at full speed ; such places as the hollow streamline nascelles behind the radial engines (*cf.* Lumsden's record of bird's nest and egg), the undercarriage, the rear aspect of the wheels, where the slip-stream would tend to create a small area of calm air, and other external structures might offer sufficient shelter to enable an insect to cling there out of the main air rush. Modern streamlining has rendered this an impossibility. On the Empire Flying Boats of Imperial Airways no area is available that is not subjected to the pressure of air passing over it at over 150 m.p.h. during flight. The more perfect the aerodynamic quality of the design the less slip-stream is created, and the closer the flow of air to all external surfaces.

In modern aircraft wings, rudders and ailerons, etc., are hollow, and possess small openings to allow of the equalisation of internal and external pressure. In the leading edges of the wings of the larger air liners are the openings of air ducts which provide the air for the ventilation of the cabin and baggage compartments. During flight air enters these openings at velocities of between 100 m.p.h. to over 250 m.p.h. according to whether the aircraft are contending with head or following winds. It is inconceivable that any insect could survive such a pressure. There is, it is true, evidence that quite frail insects are able to cling to plants and withstand remarkable wind velocities. McColloch (1917) mentions the hessian fly (*Mayetiola destructor*) clinging to plants in winds over 20 m.p.h., and Caffrey & Worthley (1927) state that the European corn borer is inactive in high winds, while Davies (1936) experimented with Aphids in a wind tunnel. They remained stationary on the glass surface of the tunnel while winds of 20–30 m.p.h. and even 70 m.p.h. were passed through it. He discovered that they possessed a small membranous pad between each claw, and another at the base of each tarsus, which presumably enabled them to resist such wind velocities ; 70 m.p.h. is however very different from 150 m.p.h. and over. Mr. H. S. Crabtree, of the Experimental Department Imperial Airways, informed the writer that wire mesh screens were originally fitted to the intakes of the air duct systems of the Empire Flying Boats. These were removed later on account of their being clogged with dust and dirt which interfered with the functioning of the system. No insects were found on those screens.

Entry of Insects on the Ground.

The exclusion of insects from aircraft while they are on the ground is possible only if all openings are sealed. The air duct system, while probably impossible to an insect during flight, offers easy ingress while stationary, particularly if the wire screens have been removed. The closure of all such apertures would be a laborious task, and where short stops are made might not be carried out efficiently. Even if complete efficiency were obtained, there is no means of preventing insects coming aboard with the luggage, staff and passengers, even immediately after the plane has been sprayed. Complete control would therefore demand a further spraying during flight, particularly as on modern flying boats it is impossible to alight on the water with all windows and hatches closed. The mooring hatch must be open, and insects might therefore escape before ground control could be carried out. Moreover, ground control is out of the question at intermediate stops where only a short time is spent, and even at night stops, to be effective, should be done before passengers and baggage leave the plane. This all makes for discomfort and delay.

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* Glick (1939) states that on several occasions insects flew into the aeroplane which he was using to collect insects in the upper air. The aircraft illustrated in his paper appear to be of the open cockpit type. According to various members of Imperial Airways technical staff, such entry by insects into the captain's cabin of a modern air liner would be extremely difficult owing to the pressure of air caused by the streamline shape of the hull or fuselage. Air does not apparently blow into the cabin when the windows are open, but streams past it, producing a sucking or vacuum effect on the opening.

Responsibility for Control.

Before attempting control of insects in aircraft the vexed question of responsibility should be settled. This cannot adequately be discussed until the full extent of the task is realised, and the types of aircraft to be dealt with are considered. There are three classes of aircraft, Transport, Military and Private.

1. *Transport Aircraft.*

The control of insects in transport aircraft should be carried out during flight. The present system, as used in various parts of the world, of spraying the aircraft by means of a " flit " type hand-pump by a member of the crew is both inadequate mechanically and subject to human error. Members of Imperial Airways staff have pointed out to the writer the difficulties connected with spraying of aircraft during flight under the present system. The responsibility rests with a member of the crew, probably a steward, for it is obviously impossible for the captain or first officer to spend the best part of half an hour just before landing in hand-flitting the ship. Should the member of the crew responsible have to contend with sick passengers, orders for drinks, or any other normal or untoward contingencies, it is obvious that his attention to efficient treatment would be impossible. Such is, in fact, frequently the case. A system of power spraying or fumigation should be built into all transport planes, possibly incorporated with the air duct system, and operated mechanically by the captain. A tell-tale should be incorporated indicating if and when spraying had been undertaken so that a glance at the instrument board would show if this had been done. The captain should pull a lever operating the system for a given time immediately after leaving port. He should repeat the operation half an hour before alighting. His duties should be confined to these two operations, and provided that his indicators showed that they had been carried out, his responsibility should end there. It should be the task of the entomologist, the chemist and the engineer, to provide a system and a chemical that will ensure 100 per cent. results in a given time. This must be the subject of further research.

2. *Military Aircraft.*

For the most part these are relatively small aircraft, and the incorporation of a mechanical system of fumigation such as has been suggested would be undesirable from the points of view of added complexity and weight, and except in the larger types of bombers and troop-carriers, would probably be impossible. Such aircraft could only be treated on the ground, and for this purpose two methods may be considered : (*a*) A fumigation chamber ; (*b*) a portable fumigating or spraying machine similar in its essentials to that incorporated in the Transport class of plane.

The fumigation chamber would only be practical at large well-equipped airports, and would be out of the question at any of the up-country military aerodromes. There would, moreover, be little point in such a system unless a gas or vapour of a deadly nature were being used. This would be undesirable both from the points of view of the staff available for operation of such plant in out of the way places, and from the difficulty of clearing aircraft of the gases, particularly if the plane should be required in a hurry.

The portable fumigating or spraying machine should be as effective as its counterpart in the air liner, and could be carried from compartment to compartment of the plane, while an attached pipe with a nozzle could be inserted into crevices and portions of the aircraft, such as wing interiors, etc., difficult of access.

3. *Private Aircraft.*

These would come under the same category as military aircraft, and could be dealt with in the same manner. The above descriptions refer only to enclosed aircraft. Open types are far less likely to harbour insects, although Glick (1939) reports such occurrences. In the writer's experience no record has yet been made of an insect taken in an open plane. It is, moreover, probable that the open type of plane will before long become relatively scarce, and long transcontinental journeys are now unlikely to be made in such craft.

From the foregoing it would seem that responsibility for transport aircraft should remain with the operating company, partly because control during flight must, when properly developed, be more efficient than ground control, and partly owing to potential difficulties involved with the latter form of control. Ground control, even if carried out with complete efficiency, must be maintained at the highest pitch by all Governments along any particular route. Differences of opinion exist as to both the necessity for such control and the method, and will probably continue to exist in the future, thus rendering real efficiency out of the question.

The control of all other types of aircraft should be the concern of the responsible Governments.

In the first case, provided that a mechanism and chemical of the required efficiency be forthcoming, permission to disembark passengers and freight, etc., could be given upon the Port Officer satisfying himself that the fumigator indicator showed that the operation had been carried out half an hour after leaving the last port of call, and half an hour before alighting. Such a system, penetrating, as it would, to every part of the internal structure of the plane, would minimise the human element to the captain of the aeroplane, and the tell-tale indicators would ensure that his memory did not fail. Existing transport aircraft not possessing such built-in apparatus could carry a portable outfit, and it would be the captain's or first officer's responsibility to see that every compartment of the plane was treated. This, however, would involve a certain amount of time on the part of the officer concerned, and might in certain circumstances be impossible. Such aircraft would therefore be classed in the second category.

In the second case, a simple procedure should be adopted as follows: All aircraft not equipped with built-in fumigating systems should be compelled by law to close all windows and hatches half an hour before alighting. (Only the larger transport flying boats will be provided with mooring hatches.) The first person to board the plane should be the fumigation official or officials with the portable plant. This should be operated immediately and before any person is allowed to disembark, including the captain or pilot. After a given period, to be determined by experiment, disembarkation could proceed. After disembarkation is finished and all formalities concluded, the plane should be closed completely and fumigation repeated. The plane should be closed until needed again. Large commercial, private or military aircraft could carry a portable spraying machine, and operate it during flight, thus obviating the initial spraying upon landing. The responsibility of carrying this out effectively should remain with the pilot, and if circumstances prevented his doing so, the normal port routine would be carried out.

Suggestions for Future Research.

Co-operation is essential, and facilities should be provided by an air line operating company to enable research to be undertaken in the actual aircraft under operating conditions. The following are the main points to be considered :—

(A) The chemical should be :—

1. Toxic to all forms of insect life.
2. As odourless as possible, and non-irritant to human beings.
3. Non-inflammable ; it is not enough to employ a high flash-point substance, as continual impregnation of fabrics and furnishings will ultimately render these highly inflammable.
4. Non-injurious to clothes, fabrics, etc.
5. Capable of being vaporised and of penetrating to every corner of an enclosed space, through cloth, wrappings, fabric, etc.

(B) The spraying or vaporising machine should be :—

- I. The built-in type.
    1. Light in weight and simple in construction.
    2. Readily accessible for cleaning and repairs.
    3. Designed to operate in every corner of the plane, including wing interiors, tail of fuselage, anchor rooms, etc.
- II. Portable type.
    1. Light and portable.
    2. Possessed of attachments for lengths of tubing and nozzles to enable inaccessible parts of the plane to be reached.

The psychological aspect of control in aircraft should not be overlooked ; thus the built-in type of machine possesses an important advantage, in that control may be carried out without the knowledge of the passengers. Provided the chemical used is more or less odourless, even the most squeamish and susceptible subjects will probably feel no ill effects, whereas the sight of an apparatus being operated in full view in the cabins might easily upset some people however innocuous the insecticide used.

The question of employing outlets to the cabins separate from the air-conditioning controls might be considered from this point of view, as the direct impingment of a stream of insecticide upon unsuspecting passengers from the air vent controls might have unfortunate effects.

Further information is needed upon the following points :—

1. Do insects enter planes during flight ? (Traps might be incorporated in the air duct system of a trans-African air liner for this purpose.)
2. The capability of different types of insect to survive air travel.

Conclusions.

The introduction of *Anopheles gambiae* into South America, either by mail steamer, destroyer or aeroplane with the unfortunate consequences thereof, recent researches upon the epidemiology of yellow fever, and the fact that aircraft offer a unique means of transport for insects, combining speed with security, have emphasised the potential danger arising from the passage of aircraft through and from the areas involved to other parts of the world.

The question as to whether certain species of insects are likely to invade aircraft has not been discussed. The writer considers this irrelevant, for *Aëdes aegypti* is considered to be a retiring species, most unlikely to leave its feeding-ground in houses and enter aircraft that may be some distance away, yet specimens have been taken in aircraft. The circumstances are such that the possibilities of the unlikely are just as much to be feared as more normal occurrences.

The latest results of the yellow fever immunity surveys in Africa and South America have indicated that the areas of endemic yellow fever are much wider in extent than was, even recently, supposed.

The discoveries of vectors of yellow fever, other than *A. aegypti*, under natural conditions, and the possibility of infecting monkeys with the virus *via* the alimentary canal, have emphasised the importance of maintaining aircraft free from all insects.

The list of insects found in aircraft suggests that it is only a matter of time before a catastrophe occurs, for the danger is not confined to medical species. In temperate regions the greater danger would appear to be from agricultural pests.

A comparison between insects found in the terrestrial zone, in the upper air, and in aircraft, indicates that insects do not enter aircraft while they are in flight, but make their entry while the planes are at rest.

A study of the literature of the flight-range of insects and the dissemination of insects by wind reveals the great difficulties of making airports free from insects.

The control of insects in transport aircraft should be undertaken during flight, and the responsibility of such control should remain with the operating company. Governments should be responsible for all other types of aircraft.

Little will be gained from further research upon the insects found in aircraft, as sufficient facts have been established indicating the importance of control measures. Research is urgently needed upon the subject, and the proposed " reserve Empire war route " for aircraft should not be initiated across central Africa to India and Australia until proper control of insects in aircraft has been achieved.

Summary.

The increase of air transport and the potential dangers therefrom, together with the related problems are investigated.

The introduction of a malarial vector from one faunal region to another, and the effects thereof are discussed.

The literature of the epidemiology of yellow fever, particularly the work done on the insect vectors and the susceptible animals is reviewed, and the implications thereof in connexion with air transport are considered.

The air communications of the world are shown as a map ; maps of Africa and South America showing the air routes and yellow fever areas are presented.

The control of air ports and aerodromes is discussed, in connexion with which the literature on the flight-range of insects, the dissemination of insects by wind, and insects and the upper air is reviewed.

A comparison is made between the insects collected from the terrestrial zone of the atmosphere and those from the upper air.

The work done upon insects found in aircraft is reviewed, and the results incorporated together with those from Khartoum in a " World List " table. The work done in Khartoum is described, and this, together with other workers' results, is analysed.

A comparison is made between insects found in the terrestrial zone, the upper air or " Plankton zone " and those found in aircraft.

The medical, veterinary and agricultural aspect of insects found in aircraft is discussed.

The control of insects in aircraft is considered and suggestions made for future research.

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COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st April and 30th June, 1939 :—

Mr. A. M. ADAMSON, Imperial College of Tropical Agriculture :—150 Isoptera ; from Trinidad.

AGRICULTURAL RESEARCH INSTITUTE, WAD MEDANI :—449 Coleoptera, 13 Parasitic Hymenoptera, 12 Formicidae, and 60 species of Coccidae ; from the Sudan.

AGRICULTURAL SUPERINTENDENT, GRENADA :—150 Isoptera.

Mr. L. S. ANDERSON :—1 Tettigoniid ; from the Red Sea.

Mr. M. D. AUSTIN :—5 Parasitic Hymenoptera ; from England.

Dr. H. F. BARNES, Rothamsted Experiment Station :—4 Parasitic Hymenoptera, from England : and 13 Diptera ; from the Punjab, India.

Dr. G. BONDAR :—6 Rhynchota ; from Brazil.

Mr. L. L. BUCHANAN :—16 Curculionidae ; from the United States of America.

Prof. P. A. BUXTON, London School of Hygiene and Tropical Medicine :—6 Formicidae ; from England : and 1,395 Diptera ; from Uganda

Mr. F. C. CAMARGO :—4 Coleoptera ; from Brazil.

CHIEF ENTOMOLOGIST, PRETORIA :—8 Diptera, 152 Coleoptera, 10 Parasitic Hymenoptera, 190 other Hymenoptera, 17 Rhynchota, 2 Orthoptera, and 20 Millipedes ; from South Africa.

CHIEF PLANT PROTECTION OFFICER, JERUSALEM :—7 Diptera, 12 Parasitic Hymenoptera, 32 other Hymenoptera, 10 species of Coccidae, and 1 species of Aphidae ; from Palestine.

COLONIAL SECRETARY, GIBRALTAR :—Samples of wood damaged by Termites.

Mr. G. H. CORBETT, Government Entomologist :—61 Coleoptera, 8 Lepidoptera, 2 Rhynchota, and 4 Dermaptera ; from Malaya.

CORYNDON MEMORIAL MUSEUM, NAIROBI :—1,567 Coleoptera, 410 Orthoptera, and 50 Dermaptera ; from Kenya Colony.

Mr. G. S. COTTERELL, Government Entomologist :—4 Diptera, 30 Coleoptera, 80 Parasitic Hymenoptera, 16 Formicidae and 4 early stages, 20 Lepidoptera, 1 species of Coccidae, and 11 other Rhynchota ; from the Gold Coast.

Mr. W. COTTIER, Entomologist :—300 Cecidomyiidae ; from New Zealand.

Mr. A. CUTHBERTSON, Entomologist :—93 Diptera and 10 early stages, 13 Coleoptera, and 7 Lepidoptera ; from Southern Rhodesia.

DIRECTOR OF AGRICULTURE, MAURITIUS :—50 Psocidae, 1,000 Mites, and 1 species of Parasitic Worm.

Mr. R. G. FENNAH, Entomologist :—102 Coleoptera, 30 Lepidoptera, 50 Isoptera, 5 Rhynchota, and 6 Snails ; from the British West Indies.

Mr. D. V. FITZGERALD :—9 Diptera, 19 Coleoptera, 7 Lepidoptera, and 7 Rhynchota ; from the Seychelles and Madagascar.

Mr. J. L. FROGGATT, Government Entomologist :—4 Diptera, 10 Coleoptera, 41 Parasitic Hymenoptera, 57 other Hymenoptera, 4 Lepidoptera, 60 Rhynchota, 15 Mites, and 1 species of Fungus ; from New Guinea.

GAME WARDEN, NAIROBI :—4 Coleoptera and 3 early stages, 7 Rhynchota, 42 Odonata early stages, 90 Ephemerid early stages, 9 Trichoptera early stages, 2 Leeches, and 3 Frogs ; from Kenya Colony.

Mr. J. C. M. GARDNER, Systematic Entomologist :—78 Diptera and 272 Parasitic Hymenoptera ; from the United Provinces, India.

Mr. S. GARTHSIDE :—6 Diptera ; from England.

Mr. P. F. GARTHWAITE, Forest Entomologist :—200 Parasitic Hymenoptera ; from Burma.

Mr. F. D. GOLDING, Government Entomologist :—9 Tabanidae, 18 other Diptera, 42 Coleoptera, 3 Parasitic Hymenoptera, 5 other Hymenoptera, 21 Lepidoptera, 4 Rhynchota, and 6 Orthoptera ; from Nigeria.

GOVERNMENT ENTOMOLOGIST, CAWNPORE :—2 species of Coccidae ; from India.

GOVERNMENT ENTOMOLOGIST, LYALLPUR :—61 Diptera and 16 pupa-cases and 150 Parasitic Hymenoptera ; from the Punjab, India.

Mr. G. V. HUDSON :—203 Coleoptera ; from New Zealand.

Dr. J. C. HUTSON, Government Entomologist :—139 Diptera and 20 cocoons ; from Ceylon.

IMPERIAL ENTOMOLOGIST, NEW DELHI :—1 species of Coccidae ; from India.

INDIAN LAC RESEARCH INSTITUTE, NAMKUM :—100 Cecidomyiidae and 29 Curculionidae ; from India.

INSTITUTE FOR PLANT DISEASES, BUITENZORG :—182 Coleoptera, 102 Lepidoptera, 1 species of Coccidae, and 34 other Rhynchota ; from the Dutch East Indies.

Mr. S. G. JARY :—8 Parasitic Hymenoptera ; from England.

Mr. G. J. KERRICH :—2 Braconidae ; from England.

Mr. T. W. KIRKPATRICK, Entomologist :—10 Diptera, 500 Parasitic Hymenoptera, and 22 Lepidoptera ; from Kenya Colony.

Mr. R. A. LEVER, Government Entomologist :—99 Diptera, 114 Coleoptera and 10 early stages, 202 Parasitic Hymenoptera, 205 other Hymenoptera, 18 Lepidoptera, 10 Isoptera, 2 species of Coccidae, 2 species of Aphidae, 110 other Rhynchota, 3 Dermaptera, 11 Odonata, 10 Trichoptera, 13 Mites, 4 Centipedes, 14 Millipedes, 22 Worms, and 10 Crustacea ; from the Fiji Islands.

Dr. E. A. LEWIS, Veterinary Entomologist :—60 Parasitic Hymenoptera ; from Kenya Colony.

Mrs. K. C. MACKAY :—1 Tenthredinid, 1 Geometrid larva, and 1 Chrysopid ; from Ireland.

Mr. JOHN MACKAY :—1 species of Aphidae ; from Ireland.

MALARIA BUREAU, HONG KONG :—25 Diptera.

Dr. L. MASI :—333 Parasitic Hymenoptera and 300 cocoons ; from Italy.

Mr. L. O. T. MENDES :—54 Parasitic Hymenoptera ; from Brazil.

Mr. A. MEUCHE :—13 Parasitic Hymenoptera ; from Germany.

Mr. H. M. MORRIS, Government Entomologist :—3 Lepidopterous larvae and 100 Isoptera ; from Cyprus.

Mr. L. A. MOUTIA :—74 Coleoptera and 56 Hymenoptera ; from Morocco, etc.

Mr. J. MUGGERIDGE, Government Entomologist :—1 species of Aphidae ; from New Zealand.

Mr. R. W. MUNGOMERY, Entomologist :—1 species of Coccidae ; from Queensland.

Musée Royal d'Histoire Naturelle, Brussels :—108 Parasitic Hymenoptera, from the Belgian Congo.

Mr. P. Nepveu :—19 Parasitic Hymenoptera ; from France.

Mr. J. Palmoni :—690 Coleoptera ; from Palestine.

Mr. E. F. Peck, Veterinary and Agricultural Officer :—3 Coleopterous larvae ; from British Somaliland.

Mr. R. T. M. Pescott, Government Entomologist :—12 species of Aphidae ; from Victoria, Australia.

Dr. M. M. Principi :—3 Parasitic Hymenoptera ; from Italy.

Dr. H. Sachtleben :—760 Coleoptera and 36 Parasitic Hymenoptera ; from various localities.

Mr. F. Schneider :—56 Diptera, 165 Coleoptera and 6 larvae, 56 Parasitic Hymenoptera, 95 other Hymenoptera, 22 Isoptera, 77 Thysanoptera, 68 Rhynchota, 3 Orthoptera, and 6 Collembola ; from Sumatra.

Selangor Museum, Kuala Lumpur :—133 Coleoptera ; from Malaya.

Nihat Shevket Iyriboz :—15 Orthoptera ; from Turkey.

Dr. A. Shulov :—170 Diptera, 6 Coleoptera, 8 Parasitic Hymenoptera, 5 Rhynchota, and 278 Orthoptera ; from Palestine.

Mr. C. Smee, Government Entomologist :—7 Diptera, 13 Parasitic Hymenoptera and 4 cocoons, 8 other Hymenoptera, 2 Lepidoptera, and 5 Rhynchota ; from Nyasaland.

Mr. J. H. Smith, Senior Research Officer :—40 Coleoptera ; from Queensland.

Mr. E. R. Speyer :—33 Diptera, 3 Coleoptera and 6 larvae, 63 Parasitic Hymenoptera, 3 other Hymenoptera and 2 species of Aphidae ; from England.

Sir Frank A. Stockdale, K.C.M.G. :—350 Isoptera ; from St. Helena.

Mr. O. H. Swezey :—5 Parasitic Hymenoptera ; from Fiji and Hawaii.

Dr. A. L. Tonnoir, Senior Research Officer :—14 Parasitic Hymenoptera ; from Australia.

Mr. K. N. Trehan :—14 Parasitic Hymenoptera ; from the Punjab, India.

Veterinary Research Officer, Entebbe :—1 *Tabanus* ; from Uganda.

Mr. J. Vinson :—22 Parasitic Hymenoptera and 4 cocoons, 5 Lepidoptera, and 3 larvae attacked by Fungi ; from Ceylon.

Dr. C. Watanabe :—76 Parasitic Hymenoptera ; from Japan.

Mr. H. Wilkinson, Entomologist :—1 species of Mite ; from Kenya Colony.

Mr. F. Wilson :—5 Diptera and 5 pupa-cases, and 2 Tenthredinidae ; from France.

Mr. E. C. Zimmerman :—2 Curculionidae ; from Guam Island.

TABANIDAE OF THE ISLAND OF TRINIDAD, B.W.I.

By J. Bequaert.

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The present enumeration of the Tabanidae known to occur in Trinidad is based almost entirely on specimens seen by myself, although I have included the very few published records apparently based on reliable identifications. None of the material was collected by me; but I am indebted for it to various museums and private collectors: Dr. J. G. Myers, Mr. D. Vesey-FitzGerald, Dr. Neal Weber, Mr. John Smart and Mr. H. Oldroyd (British Museum), Mr. L. L. Pechuman (Cornell University), and Dr. Alan Stone (U.S. Bureau of Entomology and Plant Quarantine).

The list was compiled in order to obtain a reliable basis of comparison with the Tabanid fauna of the Antilles, as a revision of the Antillean Tabanidae is now nearing completion. In that paper the relations with neighbouring faunae will be fully considered. It may be stated in brief that the affinities of the Trinidad fauna are wholly with Continental South America, not with the Antilles. All of the 23 species here listed have been found on the American mainland, but only three or possibly four occur in both Trinidad and the Antilles. These are *Chrysops variegata*, a common fly throughout Central and South America, as well as in the Greater Antilles; *Tabanus hookeri*, a species of the Greater Antilles and Barbados, also found in South America; *Tabanus ferrifer*, widely distributed in South America, but originally described doubtfully from Barbados; *Tabanus carneus*, known from Mexico and Central America, as well as from Puerto Rico (perhaps introduced by man), occurring probably also in South America proper. A fifth species, *Lepiselaga crassipes* (Fabricius), of the Greater Antilles, Central and South America, has not yet been taken in Trinidad but presumably occurs there. It is even more significant that all of the seven genera in the list are South American, while four of them have not been taken in the Antilles.

The evident South American character of the Trinidad fauna is, of course, readily explained by the close proximity of the Venezuelan mainland (less than 15 miles away), as well as by the recent geological history. Trinidad is a fairly large island (1,754 square miles), with diversified ecological conditions very similar to those of the mainland and favourable to the development of Tabanidae.

Tobago, a small dependency some 20 miles to the north-east of Trinidad, is little known entomologically. No records of Tabanidae have as yet been published from this island; but I have seen from there a few specimens of *Tabanus trilineatus*, a common species in Trinidad and South America.

1. **Chrysops variegata** (Degeer) (*C. costata*, Fabricius).

I have seen several specimens from Trinidad. It is the most common and widely distributed species of the genus in Central and South America (from southern Mexico to northern Argentina), as well as in the Greater Antilles.

2. **Chrysops tristis** (Fabricius).

I have seen a female taken in Trinidad, as well as specimens from Venezuela and British Guiana. Originally described from Cayenne, this species has been reported also from Surinam, Brazil and Bolivia.

3. Chrysops fulviceps, Walker (*C. aurofasciatus*, Kröber).

I have seen a female from Trinidad. The species is known from British Guiana, Brazil, Bolivia and Peru.

4. Chrysops auroguttata, Kröber.

I have seen the female from Trinidad (Dr. A. Balfour—Brit. Mus.), which Kröber (1930, Zool. Anz., **90,** p. 71) listed as one of the original specimens, or cotypes, the other being from Colombia ; also, a female from Port of Spain (G. A. K. Marshall—Brit. Mus.) and another " on road to Oropouche " (Dr. J. R. Dickson—Brit. Mus.). Kröber (*op. cit.*, p. 72) also described from Trinidad a var. *pallidefemorata*, scarcely separable from the typical form. I have seen typical *auroguttata* from Costa Rica, and Pechuman (1937, Rev. Ent. **7,** p. 136) reports the var. *pallidefemorata* from Panama. Pechuman's surmise that Kröber's type of the var. *pallidefemorata* came from " Trinidad Riv., Panama," and not from the island of Trinidad, is erroneous.

5. Chrysops bulbicornis, Ad. Lutz.

Originally described from southern Brazil, this species was taken in Trinidad (Dr. Percy Rendall—Brit. Mus.). I have seen it also from Bolivia.

6. Esenbeckia prasiniventris (Macquart).

I have seen a female from Trinidad, Hololu, W.R., 500 ft. (Dr. F. W. Jackson—Brit. Mus.). The species is common in Guatemala, the Republic of Honduras, Costa Rica, Panama, Colombia, Venezuela, British Guiana, Brazil and Ecuador. It was previously reported from Trinidad by Miss Ricardo (1900, Ann. Mag. Nat. Hist., (7) **5,** p. 173).

7. Selasoma tibiale (Wiedemann).

I have seen a female from Trinidad (Brit. Mus.). The species is known from Mexico, British Guiana, French Guiana, Brazil and northern Argentina.

8. Stibasoma fulvohirtum (Wiedemann).

Knab referred to this species a female from Trinidad (1913, Proc. U.S. Nat. Mus., **46,** p. 411). It is also known from Panama, Colombia, Venezuela and Brazil. Kröber's record from " Georgia " must be due to some error, as the species does not occur in the United States.

9. Stibasoma dyridophorum, Knab.

This species was originally described from Trinidad (1913, Proc. U.S. Nat. Mus. **46,** p. 410). It is not yet known from elsewhere, but Knab suggested that *Tabanus ferreus*, Walker, described from Brazil, might have been the male. What Kröber (1932, Rev. Ent., **2,** p. 299) described as " *Chelotabanus ferreus* Walker " was perhaps not the true type.

10. Dichelacera ochracea, Hine.

This species was described from Port of Spain, Trinidad, and from Mallali, British Guiana (1920, Ohio Jl. Sci., **20,** p. 318). I have seen several females collected in the Maracas Valley, Trinidad, by Dr. N. Weber. Kröber includes Brazil in the distribution, but I do not know on what evidence.

11. Tabanus (Lophotabanus) ferrifer, Walker (=*T. druyvesteijni*, Szilády).

What I here call *ferrifer* is Szilády's and Kröber's *druyvesteijni*, which is, in my opinion, a synonym. I have seen several males and females from Trinidad (J. G. Myers, N. Weber, R. A. Lever, Dr. J. R. Dickson, L. E. Cheesman), which was the original locality for the male of *druyvesteijni* (1926, Biol. Hung., **1**, pt. 7, p. 26). It is one of the most common species on the American continent. I have seen it from British Honduras, Panama, Colombia and Venezuela; and it has been reported from Dutch Guiana, Brazil, Bolivia, Paraguay and northern Argentina. Walker described *ferrifer* doubtfully from Barbados, but his type may have come from Trinidad. It has never been taken since in the Antilles.

12. Tabanus (Lophotabanus) xipe, Kröber (=*Lophotabanus surinamensis*, Kröber 1929; not *Tabanus surinamensis*, Macquart 1838).

I have seen three females from Trinidad, one collected by T. W. Cameron (Brit. Mus.), another by N. A. Weber (near Rio Claro), and the third by Urich (Brit. Mus.). It is widely distributed in South America, as I have seen it also from Panama, Colombia, Venezuela, Brazil and Peru. Kröber described it from Surinam, French Guiana and Venezuela. It is perhaps not specifically distinct from *T. albocirculus*, Hine, of Costa Rica, which seems to differ only in the blackish, not reddish-brown, abdomen. I even have some doubts as to its distinctness from *T. oculus*, Walker, which seems to differ only in having the fourth posterior cell closed and petiolate, scarcely a reliable character in TABANIDAE. *T. xipe* varies in total length from 9·5 to 17 mm. Two of the females from Trinidad are smaller than most of those I have seen from the continent, but a few from Panama and Venezuela are no larger; the third female from Trinidad is of the usual size (16·5 mm.).

13. Tabanus (Chlorotabanus) mexicanus, Linnaeus.

This species was recorded from Trinidad by Knab in the paper in which he pointed out for the first time its true characters and those of its near allies (1916, Insec. Insc. Menst., **4**, p. 96). The occurrence in Trinidad is therefore beyond doubt. I have seen it from Colombia, Panama, Costa Rica and the Republic of Honduras. The related *T. inanis*, Fabricius, differing by the lack of spots in the wings, no doubt will be found in Trinidad also, as it is even more common on the mainland than *mexicanus*. Ad. Lutz' supposed *mexicanus*, from Venezuela (1928, Est. Zool. Paras. Venezolanas, p. 56, Pl. ix, fig. 6), was *T. inanis*, the figure showing no spots in the wings. *T. viridis* (Enderlein) is not a synonym of *T. inanis* (see below). *T. mexicanus* is structurally very similar to *T. inanis*, in the shape of the antennae (of both sexes) as well as in that of the frons (in the female). In the male of *mexicanus* the holoptic eyes are separated at the vertex by a deep, open notch, without intervening callosity.

14. Tabanus (Ommallia) viridis (Enderlein) (=*Ommallia viridis*, Enderlein, 1925, Mitt. Zool. Mus. Berlin, **11**, pt. 2, p. 389, ♂; *Ommallia thiemeana*, Enderlein, 1925, *l.c.*, ♀).

O. viridis, described from the " Tierra caliente " in the Cordilleras of Colombia, is said by Kröber (1930, Zool. Anz., **87**, p. 17) to be identical with *T. inanis*, Fabricius. He claims that in *T. inanis* the shape of the third antennal segment varies all the way from almost toothless to bearing a prong nearly as long as the basal portion. Kröber seems to have confused under *inanis* three species, distinct not only by the shape of the antennae in both sexes, but also by other characters, such as the structure of the frons in the female; all three species being grass-green and with unspotted wings. Of what I call *T. viridis*, I have seen two males and one female from Trinidad: St. Augustine, 1 ♂ and 1 ♀ (Dr. C. L. Withycombe—Brit. Mus.); Brasso, 1 ♂ (N. Weber). In these the third antennal segment is narrow basally and provided with a long, erect prong; in the male, the holoptic eyes are narrowly separated at the vertex, with an intervening callosity ; in the female, the frons is four to five times as long as wide, with a narrow, denuded, greenish-yellow basal callus extending upward in a short ridge. All three specimens have a long appendix to the fork of the third vein, a peculiarity given by Enderlein in his key as one of the characters of his genus *Ommallia.* The Trinidad female is certainly conspecific with the two males from the same locality. As it agrees quite well with the description of *Ommallia thiemeana*, Enderlein (based on a female, from Colombia), I regard this as the other sex of *O. viridis* (originally based on the male only).

In *T. inanis*, the third antennal segment is very broad oval basally, and very slightly or scarcely angular above ; in the male, the holoptic eyes are separated at the vertex by a deep, open notch, without intervening callosity ; in the female the frons is six to seven times as long as wide, without any trace of a basal callus. In 23 *T. inanis* seen, from Costa Rica, Panama, Colombia, French Guiana, British Guiana and Brazil, only one has a trace of an appendix to the fork of the third vein, in one wing only.

A third green species, with unspotted wings, of which I have a male from Paraguay, has the antenna shaped as shown by Kröber (1930 *l.c.*) in his fig. 12, being broader and shorter than in *T. viridis*, but with a prominent tooth ; the holoptic eyes have an intervening callosity at the vertex ; there is no appendix to the fork of the third vein. This is possibly the male of the species described from the female by Enderlein as *Ommallia brevihamus* (1925, *op. cit.*, p. 390 ; Colombia). *Tabanus viridescens*, Kröber (1931, Konowia, **10,** p. 296 ; Surinam) appears to be a synonym either of *T. brevihamus* or of *T. viridis*.

15. **Tabanus (Leucotabanus) leucaspis,** Wiedemann.

One female, Maracas, Trinidad (J. G. Myers—Brit. Mus.). A common and widely distributed species on the American continent, from southern Mexico to northern Argentina, but not known from the Antilles. The supposed *T. leucaspis* from Arizona has been described as a distinct species, *T. ambiguus* (Stone).

16. **Tabanus (Macrocormus) sorbillans,** Wiedemann.

I have seen two males and three females from Trinidad (M.U. Beattie, R. A. Lever, C. L. Withycombe, D. Vesey-FitzGerald). More definite localities are St. Augustine and Tacarigua. Kröber also recorded it from Trinidad (1930, Zool. Anz., **87,** p. 11). I have seen it from Paraguay, and there are records from Brazil. In this species the first posterior cell (R_5) is more or less narrowed apically, sometimes almost closed at the margin.

17. **Tabanus (Amphichlorops) unicolor,** Wiedemann.

I have seen a male from Mayaro Bay, Trinidad, taken at light (D. Vesey FitzGerald). The species is known from Panama, Venezuela, British Guiana, Brazil and Peru.

18. **Tabanus (Neotabanus) hookeri,** Knab.

This species, readily recognized by the bare and shiny subcallus, is fairly common in Trinidad, whence I have seen females and males. It occurs in the Greater Antilles and, on the Continent, I have seen it from Venezuela, Colombia, Paraguay and northern Argentina ; also from Barbados. Surcouf and Kröber credit the specific name by error to Townsend. It may have been described under some earlier name from the mainland.

19. **Tabanus (Neotabanus) trilineatus,** Latreille.

Apparently a common species in Trinidad : St. Augustine, St. Clair, etc. I have seen three females and eight males (J. G. Myers, N. Weber, C. L.Withycombe,

H. A. Ballou, P. L. Guppy, R. A. Lever). One female and one male, rather poorly preserved, from Tobago (Old Grange Tower, Capt. A. K. Totton, and Lambeau Hill, Dr. J. Smart) are not separable from Trinidad specimens. I have followed the late Major Austen's identification in applying the name *trilineatus* to this species, which is fully characterized in the subjoined Key. The males here associated with female *trilineatus* have the mid and hind femora extensively black basally, while the females have them almost entirely yellowish. Yet these males are quite certainly not of any of the other trivittate species I have seen from Trinidad. The species here called *trilineatus* is certainly distinct from the North American *T. lineola*, Fabricius, which has the frons narrowed below, not nearly parallel-sided.

20. Tabanus carneus, Bellardi.

I refer to this species two females and one male from Trinidad (♀♂ L. E. Cheesman ; ♀, Siparia, Dr. J. R. Dickson—all Brit. Mus.). They are indistinguishable from a series of specimens I collected in the Republic of Honduras. I also refer to it a female taken in Puerto Rico, where the species may be a recent introduction by man. The characters of what I call *carneus* are shown in my Key. The late Major Austen labelled one of the Trinidad females, *T. modestus*, Wiedemann, but the description of that species gives the abdomen as blackish and the hind femora black at the base, two features not found in the Trinidad flies. As Kröber recognized, the description of *T. modestus* agrees best with *T. plangens*, Walker.

21. Tabanus (Neotabanus) appendiculatus, Hine.

I refer to this species two females from Trinidad, one from Port of Spain (Dr. F. A. Phillips—Brit. Mus.), the other from St. Augustine (N. Weber). Both have the appendix in the wing. One of these was identified as *T. occidentalis*, Linnaeus, by the late Major Austen, who also wrote on the label, as synonyms, *T. consequa*, Walker 1850, and *T. importunus*, Macquart 1847 (not of Wiedemann 1828). As none of these three species has been recognized beyond doubt, I prefer to use Hine's name, the description of which fits the Trinidad specimens in every respect.* Moreover, I have many specimens of *T. appendiculatus* from the Republic of Honduras, Guatemala, Colombia, Brazil and Venezuela. All these agree with the Trinidad flies and have the characters given in my Key. My *T. appendiculatus* is obviously distinct specifically from what I here call *T. carneus* and seems to be part of what Kröber called *T. lineola*. The true North American *T. lineola*, Fabricius, has the fore coxae and most of the mid and hind femora greyish black, and the basal portion of the third antennal segment shorter and broader. As *T. appendiculatus* is one of the more common Neotropical Tabanids, no doubt it will eventually be given an older name. In what I regard as the male of *T. appendiculatus* (from the Cauca Valley, Colombia) the facets of the eye are as in *T. carneus*, but the upper two-thirds of the eye are densely pilose.

22. Tabanus (Neotabanus) ochrophilus, Ad. Lutz (1914, Mem. Inst. Osw. Cruz, **6,** p. 49, ♀♂ ; 1928, Est. Zool. Paras. Venezolanas, p. 56, Pl. ix, fig. 10, ♀).

I refer to this species, with some doubt, a female from Trinidad (T. W. Cameron —Brit. Mus.) differing from the other trivittate specimens taken on the island in having the margins of the median stripe distinctly serrate, as shown in Lutz' figure of *ochrophilus*. Surcouf treated *T. ochrophilus* as a *nomen nudum* ; but the original reference contains a brief descriptive phrase : " Da das Abdomen bei dieser Art mehr ockerfarbig ist, als bei den anderen [*i.e.* the group of *T. triangulum*], welche ebenfalls drei hellen Streifen auf dem Abdomen zeigen, nenne ich sie *N. ochrophilus*." The species may, moreover, be recognized from Lutz' coloured figure of 1928. It was originally based on two males and five females bred from pupae found near Manguinhos (Rio de Janeiro), Brazil. Lutz later referred to it specimens from various other Brazilian States (São Paulo, Rio Grande do Sul, Minas Geraes, Bahia), Paraguay and Venezuela.

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* The type of *T. occidentalis* is probably lost. What Kröber (1933, Rev. Ent., **3**, p. 360) called the " type " was Wiedemann's specimen, not Linnaeus'. Moreover, Kröber's *T. occidentalis* is seemingly not the species from Trinidad here called *T. appendiculatus*, since he says that the mid and hind femora are black at the base and that the eyes of the male are bare. The types of both *T. consequa*, Walker, and *T. importunus*, Macquart, are at the British Museum. They were examined by Kröber, but he was unable to reach a definite conclusion regarding their identity (1933, *op. cit.*, pp. 353, 361). His statements that the frons of *T. consequa* is about 3½ times as high as wide above and markedly narrowed below, that the mid and hind femora are entirely reddish yellow, and that there is an appendix in one of the wings, agree well with *T. appendiculatus*, but a direct comparison of specimens would be needed to synonymize the two. *T. importunus*, in very poor condition, may be the same, although Kröber is inclined to refer it to his *occidentalis* ; but as the name is preoccupied in *Tabanus*, the matter is of little nomenclatorial importance.

The *Tabanus* with trivittate abdomen (*Neotabanus*, Ad. Lutz 1909, not of Ricardo 1911 ; *Taeniotabanus*, Kröber 1932) are among the most difficult insects to deal with. In the Neotropical Region, there are at least a dozen species of this type, each with distinctive structural characters, notably of frons and antennae. As these characters are not or inadequately mentioned in most published descriptions, identifications remain uncertain. The only attempt at a comprehensive treatment is by Kröber (1933, Rev. Ent., **3**, pp. 337–367) and it is far from satisfactory. In Trinidad the trivittate group is represented by five readily recognized species. These I have listed above as *T. hookeri*, *T. carneus*, *T. trilineatus*, *T. appendiculatus* and *T. ochrophilus*. In order to allow other workers to recognize what is meant here by these names, I subjoin a Key embodying all important characters. Future collectors should note the banding of the eyes in life, as this may provide reliable specific differences.

1. Subcallus bare, shiny honey-yellow in both sexes. Mid-dorsal stripe widened at the apex of each segment, consisting of a series of triangles ; lateral stripes broken up into oblique spots. Female : frons about three times as high as wide, slightly narrowed below. Male : upper two-thirds of eye hairy and with the facets much larger than those of lower third. Length 9 to 12 mm.... *T. hookeri*

Subcallus normally dull and covered entirely with pollinosity 2

2. Female : frons parallel-sided, about four times as high as wide ; basal callus brownish, rectangular, slightly higher than wide. First antennal segment much swollen apically above ; third segment with the basal portion longer than greatest width, the apical annuli shorter than the basal portion. Mid and hind femora mostly reddish yellow, fore coxae greyish black. Thorax mostly covered with white hair ; stripes of abdomen covered with silvery-white hair, the median stripe regular, parallel-sided, the lateral stripes nearly straight. Wing hyaline, normally without appendix to fork of third vein. Male : upper half of eye with the facets slightly larger than in lower half and densely hairy ; mid and hind femora blackish-grey over basal third. Length 12 to 15 mm....... *T. trilineatus*

Female : frons more or less narrowed below : if the frons is nearly parallel-sided, the first antennal segment is not conspicuously swollen above and the median stripe of the abdomen is not parallel-sided 3

3. Female : median stripe of abdomen not parallel-sided, but widened at the apex of each segment so as to form a series of truncate triangles. Frons very slightly or scarcely narrowed below, five to six times as high as wide ; basal callosity black, elliptical, much higher than wide. Basal portion of third antennal segment only slightly or not longer than wide, the annulate portion nearly as long as basal portion. Fore coxae greyish black ; mid and hind femora black over basal third to half. Wing very faintly clouded near the cross-veins, the fork of third vein normally without appendix. Length 11 mm. Male unknown .... *T. ochrophilus*

Female : median stripe of abdomen regular, parallel-sided. Frons markedly narrowed below, sometimes almost twice as wide at occiput as at subcallus. Mid and hind femora entirely reddish yellow ; fore coxae reddish yellow...... 4

4. Female : frons about four to five times as high as wide below ; basal callosity yellowish brown, only slightly higher than wide. Pubescence of thorax and abdominal stripes yellowish grey. Wing nearly hyaline, the fork of third vein normally without appendix. Length 12 to 14 mm. Male : facets of upper two-thirds of eye very much larger than those of lower third, the eye entirely bare...*T. carneus*

   Female : frons five to six times as high as wide below ; basal callosity dark brown, rectangular, much higher than wide. Pubescence of thorax and abdominal stripes yellowish grey. Wing somewhat clouded, the fork of third vein normally with appendix. Length 13 mm. Male : upper two-thirds of eye densely hairy, with very large facets .... *T. appendiculatus*

23. Acanthocera marginalis, Walker.

I have seen one specimen from Trinidad. The species was originally described from Brazil and has been recorded from French Guiana.

ON THE DISTRIBUTION OF *LEUCOPTERA DARICELLA* (MEYR.); WITH THE DESCRIPTION OF A NEW LEAF-MINER FROM COFFEE.

By Roger Washbourn, B.A.

Department of Entomology, British Museum (Nat. Hist.)

(Plate XIV.)

Introduction.

The Lyonetiid moth *Leucoptera daricella* (Meyr.) was described in 1880,[1] from two specimens taken at Rosewood, Queensland. It was assigned to the genus *Crobylophora*, Meyr., which is intermediate between *Bucculatrix*, Z., and *Stegommata*, Meyr. (=*Lyonetia*, Hübn.). In 1893 two more specimens were recorded from Queensland,[2] and since that time the range of the species has been gradually extended by records from other parts of the world. In 1894 the species was recorded by Meyrick[3] from the Shan States, Burma. In 1918 he recorded it from Natal,[6] and at the same time made it an Indian species by sinking under *L. daricella* two species, *Crobylophora staterias*, Meyr., and *C. onychotis*, Meyr., previously known from that country.[4, 5] Two further references to *daricella*, as an Indian species, were made by Fletcher.[7, 9] In 1921 the latter reported it as occurring abundantly on *Plumbago*, and in 1933 he described the larval habits and stated that the species *daricella* (Meyr.) should be placed in the genus *Leucoptera*, Hübn. In 1933 a species of Lyonetiid was found to be a serious pest mining the leaves of coffee in Tanganyika. Specimens were sent to the late E. Meyrick, who named them *Leucoptera coffeella* (Guér.), a species which they manifestly were not. They did, however, bear considerable resemblance to *L. daricella* and they were sent out from the British Museum under this name. In 1935,[11] this species was reported as the predominant pest in Tanganyikan coffee plantations.

Early in 1938 an inquiry reached this Museum concerning the exact differences between the species of *Leucoptera* found on coffee. The investigation to answer this inquiry showed that there was much confusion concerning *Leucoptera daricella*, and to clear it up, an analysis has been made of all the material standing under this name in the collections of the British Museum and of the late E. Meyrick.

Analysis of Material standing in British Museum.

The specimens standing under the name *Leucoptera daricella* (Meyr.) are derived from various sources, and may conveniently be classified as follows :—

1. The cotypes of *L. daricella*, together with the two further specimens of this species recorded from Duaringa, Queensland, in 1893, three further specimens unrecorded, from the same locality, dated 1885, and one unrecorded specimen from Brisbane, dated 1897.
2. A number of Indian specimens, all under *L. daricella*. These include :—
    - (*a*) Three specimens of the four recorded from the Shan States, Burma, in 1894, and named by Meyrick ;
    - (*b*) The cotypes and type of the two species sunk by Meyrick under *L. daricella*, *Crobylophora staterias*, Meyr., and *C. onychotis*, Meyr.

3. A number of African specimens, including :—
    - (*a*) One specimen which may be that from which the first African record was made. It is labelled in Meyrick's handwriting " Umkomaas, Natal. A.J.T.J. 1914." (Meyrick's label has since been lost.)
    - (*b*) A second single specimen, labelled " *daricella* (Meyr.) Kabete, E. Africa, H. E. Box, i. 1922, larva on coffee leaves." (There does not appear to be any reference in the literature to this specimen.)
    - (*c*) A long series bred from coffee in Tanganyika, all from A. H. Ritchie, with various dates and localities. These are the specimens from which the infestation of coffee by *daricella* was reported in 1933.
    - (*d*) Part of this series (specimens from Moshi, 17 Nov. 1934) was bred from *Cremnospora africana* and might give rise to the report that this plant was an alternative host for the coffee-feeding *L. daricella*.
4. In addition to these specimens, a number have been sent from Africa, through the kindness of Messrs. Kirkpatrick and Notley, while Mr. T. Bainbrigge Fletcher has kindly lent specimens taken in India.

Examination of the Material.*

1. *Leucoptera daricella* (Meyr.). Type and associated specimens (B.M. Nos. 1250–1257). The two cotypes are females (B.M. 1250, 1251), and were taken at Rosewood, Queensland, in 1879, in thick subtropical scrubs. I cite No. B.M. 1250 as the lectotype.

Original description (Meyrick : Proc. Linn. Soc. N.S.W., **5,** 1880, p. 178).—" ♂ [this is wrong ; both are females] 3¼″. Head, palpi, antennae, thorax, abdomen and legs snow-white ; all tarsi with three blackish rings. Forewings snow-white, with two slender short oblique black costal streaks, first in middle, second immediately beyond it, closely strewn about which are a few irregular blackish and ochreous scales ; a rather large circular thickened silvery metallic spot on anal angle, partially black edged ; cilia white, with a faint fuscous spot in costal cilia, from which proceeds a clear black line round apex, terminating abruptly just beyond it. Hindwings and cilia white."

To this description I add figures of the forewing venation, forewing pattern, and female genitalia, all taken from the specimen cited above as the lectotype (figs. 1–4 and Plate XIV, *b*). I also give a figure of the male genitalia of one of the specimens associated with the type (B.M. 1254), which I regard as conspecific with the type. The main points of note in these structures are as follows :—

(i) There are four veins running from the cell to the termen of the forewing, and five from the cell to the costa (text fig. 1, *a*). Two pairs of these are stalked from a common base ; of one pair both branches go to the costa, of the other, one vein goes to the costa and the other to the termen.

(ii) In the male, the 8th abdominal sternite forms a pair of feeble lobes which partly cover the genitalia (text fig. 2, *a*). The tegumen is much reduced, and the uncus absent. The valves have a characteristic shape. The 8th abdominal tergite forms a pair of dorsal flaps, covering genitalia dorsally.

(iii) The female genitalia are characterised by the elevation of the ductus bursae on to a long sclerotised spur (text figs. 3, *a* ; 4, *a*). The lobes of the ovipositor have a characteristic shape.

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* Throughout this work I have followed the nomenclature of Meyrick[12] for the superficial structure, that of Mehta[10] for the male genitalia, and that of A. Busck[2] for the female genitalia.

2. *Leucoptera daricella* (Meyr.). Indian specimens.

(*a*) Specimens taken at Mone, Shan States, Burma, dated 1888 (B.M. 1265, 1266, 1270).

These three specimens may represent two species, but I am of the opinion that none of the three is *daricella*. The genitalia are quite distinct from those of the types of *daricella*, while the forewings have in one case two veins, and in the remainder one vein, fewer than those of *daricella*. In other respects, also, the venation is different from that of *daricella*.

(*b*) Type specimens of species sunk by Meyrick under *L. daricella*.

(i) *Crobylophora staterias*, Meyr. The type series consists of three cotypes, bred at Peradenyia, Ceylon, on *Plumbago capensis* in July 1902. These specimens are in the British Museum, and, since it is impossible to decide to which specimen the original description refers, I cite female No. B.M. 1269 as the lectotype, Nos. 1268 and 1272 being paratypes.

Original description (Meyr., J. Bombay, N. H. Soc. **16,** 1905, p. 613).—"♂. 5–6 mm. Head, antennae, and thorax shining white. Forewings lanceolate; shining white; three oblique slightly converging dark fuscous lines from costa beyond middle, directed towards tornal spot but not reaching it, space between two anterior pale whitish-ochreous; a dull round golden-metallic raised tornal spot, edged laterally with blackish, and anteriorly faintly ringed with pale yellowish; cilia ochreous-whitish, with three fine fuscous lines, innermost dark fuscous. Hindwings and cilia whitish."

To this description I add figures of the wing pattern, wing venation, and male and female genitalia taken from B.M. 1272, 1259, 1269, specimens which I have carefully examined, and which are either types or in my opinion conspecific with the type (text figs. 1, *b*; 2, *b*; 3, *b*; 4, *b*, and Plate XIV, *c*). On the evidence afforded by these studies, I am of the opinion that Meyrick was mistaken in sinking *Crobylophora staterias*, Meyr., under *daricella* (Meyr.), and I think that *C. staterias* must be regarded as a good species. The most obvious differences in the structure of *C. staterias* compared with that of the types of *L. daricella* are as follows:—The presence of a pale yellow ring round the tornal spot of the forewing; the absence from the forewing of one of the veins present in *daricella** (text fig. 1, *b*, *cf.* 1, *a*); the presence and size of a conspicuous uncus (text fig. 2, *a*, *b*); the singleness of the 8th abdominal tergite; the more or less triangular shape of the ovipositor lobes in *C. staterias* as contrasted with the more rectangular shape of the lobes of *L. daricella* (text fig. 3, *a*, *b*).

The constancy of these structures has been confirmed by the examination by a number of other specimens of the same species, kindly lent by Mr. T. B. Fletcher.

(ii) *Crobylophora onychotis*, Meyr. The type (B.M. 1260) is a male, taken in the Khasi Hills, Assam, in November 1906. Associated with it is a female, taken in the same place a month earlier. Though the two specimens are very much alike, I do not think myself justified in regarding them as male and female of the same species, and I therefore give figures and notes on the structure of the male only.

Original description (Meyrick, Exotic. Micr. **1,** 1912, p. 345).—"♂. 8 mm. head, thorax, and abdomen white. Forewings lanceolate, apex somewhat produced, acute; shining white; a pair of fine parallel very oblique dark fuscous lines from middle of costa enclosing a pale yellowish streak, directed toward tornal spot and reaching halfway towards it; a third somewhat shorter dark fuscous line near beyond and parallel to these; a round pale golden-metallic tornal spot edged on each side by a blackish dot : cilia white, on costa with a fine dark fuscous basal line and a second oblique line converging with it to a point at apex, thence continued to form a hook, a third dark fuscous line at tips above apex, a faint pale brownish shade running across these above apex and continued as an apical bar. Hindwings and cilia white."

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* In some specimens of *C. staterias* it appears that two veins are missing from the forewings.

I am of the opinion that this species also is to be regarded as a good species, and that it is not conspecific with either *L. daricella* (Meyr.) or *C. staterias*, Meyr. I base my opinion on the following evidence :—Though resembling *C. staterias* in having fewer veins in the forewing than *L. daricella*, it differs from the former in that the pair of veins which are forked round the apex arise from much nearer the cell than they do in *C. staterias* ; the male genitalia are very complex, and the 8th abdominal sternites have the appearance of strong jaws, the structure being obviously distinct from that of the foregoing species.

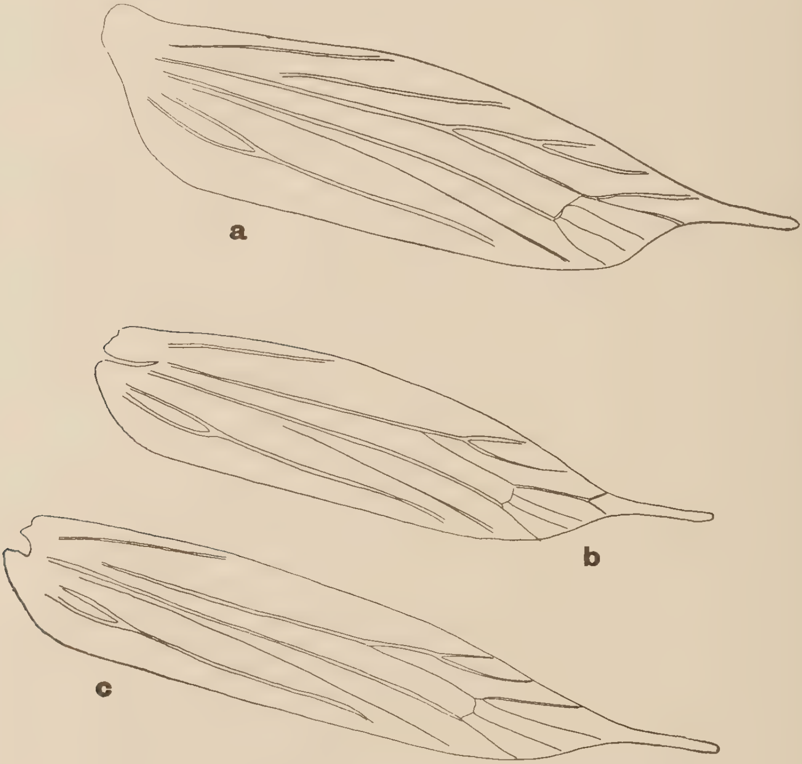

Fig. 1. Forewing venation of **a,** *Leucoptera daricella* (Meyr.) ; **b,** *Crobylophora staterias*, Meyr. ; **c,** *Leucoptera caffeina*, sp. n. (all × 35).

3. *Leucoptera daricella* (Meyr.). African specimens.

(*a*) I have examined the single specimen (B.M. 1277) which was placed under "*daricella* (Meyr.)" in Meyrick's Collection and which is labelled "Umkomaas, Natal, A.J.T.J. 1914." It is in bad condition and the abdomen is absent, but on the evidence of the wing venation, I believe that it is not conspecific with the type of *L. daricella*.

(*b*) The second single specimen (B.M. 1276) identified as *L. daricella* (Meyr.) for Box, has forewing venation and genitalia distinct from those of the type of *daricella*, and I do not think that it is this species.

(*c*) This series, which consists of a number of specimens bred from coffee, in my opinion, represents a new species. The description, which follows, is taken from a fresh series from Tanganyika, bred by Notley in Aug. 1938 ; I propose the name *Leucoptera caffeina*, sp. n., and I believe that it is conspecific with the series sent to the British Museum by A. H. Ritchie in 1932.

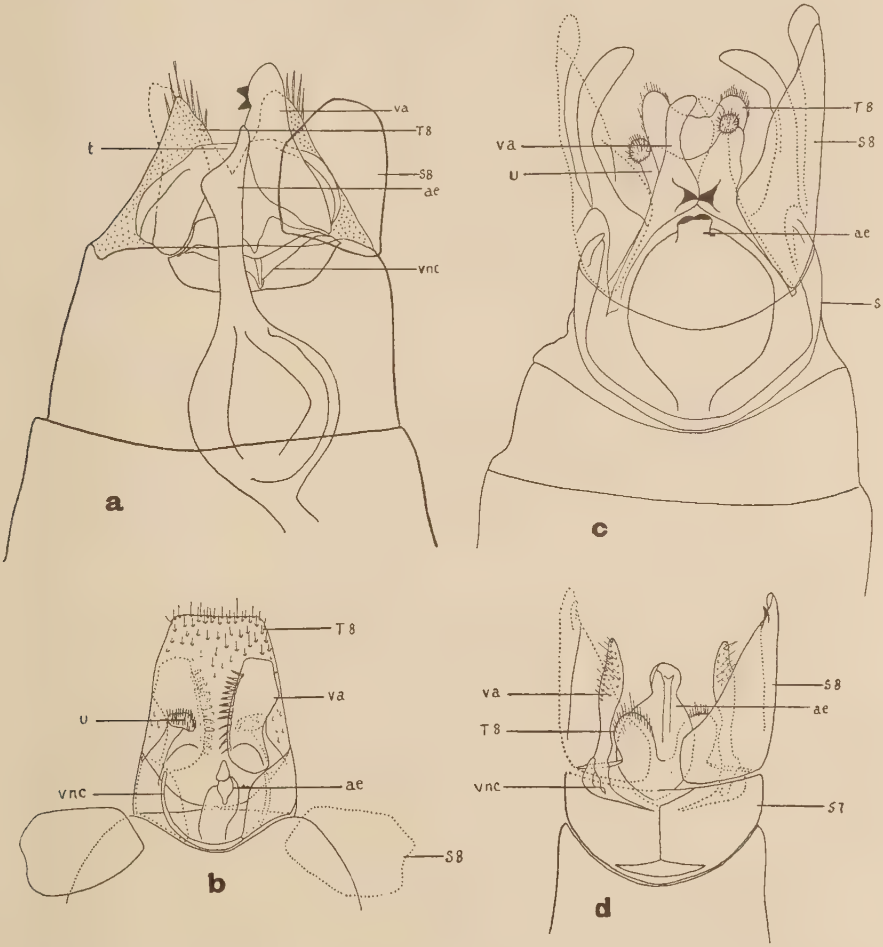

Fig. 2. Male genitalia of : **a,** *Leucoptera daricella* (Meyr.) (8th sternite omitted on left) ; **b,** *Crobylophora staterias*, Meyr. ; **c,** *Crobylophora onychotis*, Meyr. ; **d,** *Leucoptera caffeina*, sp. n. (all × 65) ; va, valvae ; vnc, vinculum ; ae, aedoeagus ; t, tegumen ; u, uncus ; S8, 8th abdominal sternite ; S7, 7th abdominal sternite ; T8, 8th abdominal tergite

Leucoptera caffeina, sp. n. (Text figs. 1, *c*; 2, *d*; 3, *c*; 4, *c*; and Plate XIV, *a*).

Head: clypeus with short, glossy white scales; frons crowned with a dense crest of erect, touzled white hair-scales. *Antennae* less than the length of the forewing, basal joint expanded, forming a broad eye-cap covered with glossy white scales; flagellum greyish. *Thorax*: tergum white, prothorax with two bunches of white hair-scales, arising from the front of each pleuron, directed backwards and extending as far as the mesothorax. *Palpi*: labial palpus reduced to a small downward pointing scale; maxillary palpus and tongue indistinguishable. *Legs*: all legs covered with short white scales; femur of first pair marked grey on outside, tibia and tarsus medium grey, with a brownish shade; tarsal joints of second and third pairs of legs marked with very dark brown spots, those on the penultimate joint of the third tarsus being especially distinctly marked; on the tibia of the third pair of legs, there is a thick even coat of long white hairs arising on the outside of the leg, on the inside a single dense tuft of long white hair scales, equal in length to the tibia.

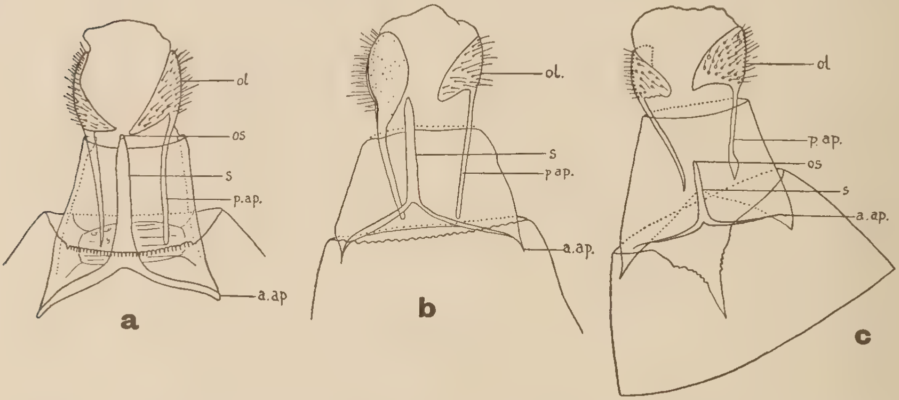

Fig. 3. Female genitalia of **a**, *Leucoptera daricella* (Meyr.); **b**, *Crobylophora staterias*, Meyr.; **c**, *Leucoptera caffeina*, sp. n. (all × 65); ol, lobe of ovipositor; os, ostium; s, spine; a.ap, anterior apophysis; p.ap, posterior apophysis.

Wings.—Forewings white, with long cilia round dorsum and termen. Markings to costa: (A.1) a very thin dark chocolate line from middle, running to the centre of the wing, which it reaches at about 2/3 of the costal length; (A.2) touching, and running alongside of the above a slightly broader band of yellow, sometimes pale, or obliterated with dark colour, sometimes expanded to a small area of yellow in the centre of the wing; (A.3) a second thin dark chocolate band bordering the yellow band A.2; (A.4) somewhat nearer the apex, a third thin dark chocolate band converging with the previous three markings, sometimes bordered yellow and dark chocolate like the above. Markings to termen: (B.1) at tornus a small dark grey shining area, sometimes very small, with a few black scales on inner and upper side; (B.2) inside this there may sometimes be a small rectangular area of yellow; (B.3) directly above the dark tornal area (B.1) there may be a few light grey scales towards the centre of the wing. Markings in cilia: (C.1) costal cilia short, taking part in costal markings; (C.2) apical cilia heavily marked to sinuate dark chocolate bands converging at apex; (C.3) between these two bands may be various shades of yellow; (C.4) cilia of termen long, white. Hindwings, white, lanceolate, with long cilia.

Genitalia (fig. 2, *d*).—Male : valves reduced, club-shaped, with short bristles on outer and upper sides ; sternite of segment 8 modified into a triangular valve-like structure bearing on the lower side a single tooth towards the apex ; penis large with a considerable sac ; eighth tergite in the form of circular lobes, bearing hairs ; vinculum much reduced ; uncus absent. Female (fig. 3, *c*) : eighth sternite cleft asymmetrically, ductus bursae short, anterior apophysis short, ovipositor lobes spade-shaped, asymmetrical ; posterior apophysis long.

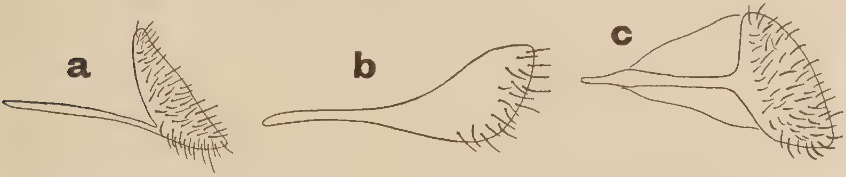

Fig. 4. Female genitalia. Lobes of ovipositor of **a,** *Leucoptera daricella,* Meyr. ; **b,** *Crobylophora staterias,* Meyr. ; **c,** *Leucoptera caffeina,* sp. n. (all × 107).

This species is described from 19 examples taken by Notley at Lyamungu, Moshi, Tanganyika Territory, in August 1938. Of these specimens I choose No. B.M. 1282 as the Type and No. 1280 as the female allotype. These and the paratypes (Nos. B.M. 1278–1285, 1287–1297) are in the British Museum.

(*d*) I have also examined the specimens (B.M. 1298–1300) which were bred by A. H. Ritchie from *Cremnospora africana*, and from which it might be thought that this plant was an alternative food-plant for the coffee-feeding species. Though these two species are very much alike, I believe that the insects from *Cremnospora* are not conspecific with *L. caffeina*, sp. n. The male genitalia, though fundamentally very much alike, show differences in the shape of the valves and of the lobes of the eighth sternites. The question whether this species can also attack coffee can obviously be answered only by experiment.

Summary.

1. An examination has been made of all specimens labelled *Leucoptera daricella* (Meyr.), standing in the collections of the British Museum and of the late E. Meyrick.

2. *Crobylophora staterias*, Meyr., and *Crobylophora onychotis*, Meyr., two species previously regarded as synonymous with *Leucoptera daricella*, are thought to be good species. The specimens of the former, which were bred from *Plumbago*, have been received from India and Ceylon ; the latter is an Indian species.

3. A new African species, *Leucoptera caffeina*, Washbn., is described, which causes damage to coffee trees.

4. Records of *Leucoptera daricella* have been investigated, and, as a result, the writer is of the opinion that this species has not yet been recorded outside Australia, and that records from Africa, India and Burma, prove unsubstantiated.

5. Lectotypes are cited of the species *Leucoptera daricella* (Meyr.), *Crobylophora staterias*, Meyr., *Crobylophora onychotis*, Meyr., and these are in the British Museum (Natural History), London.

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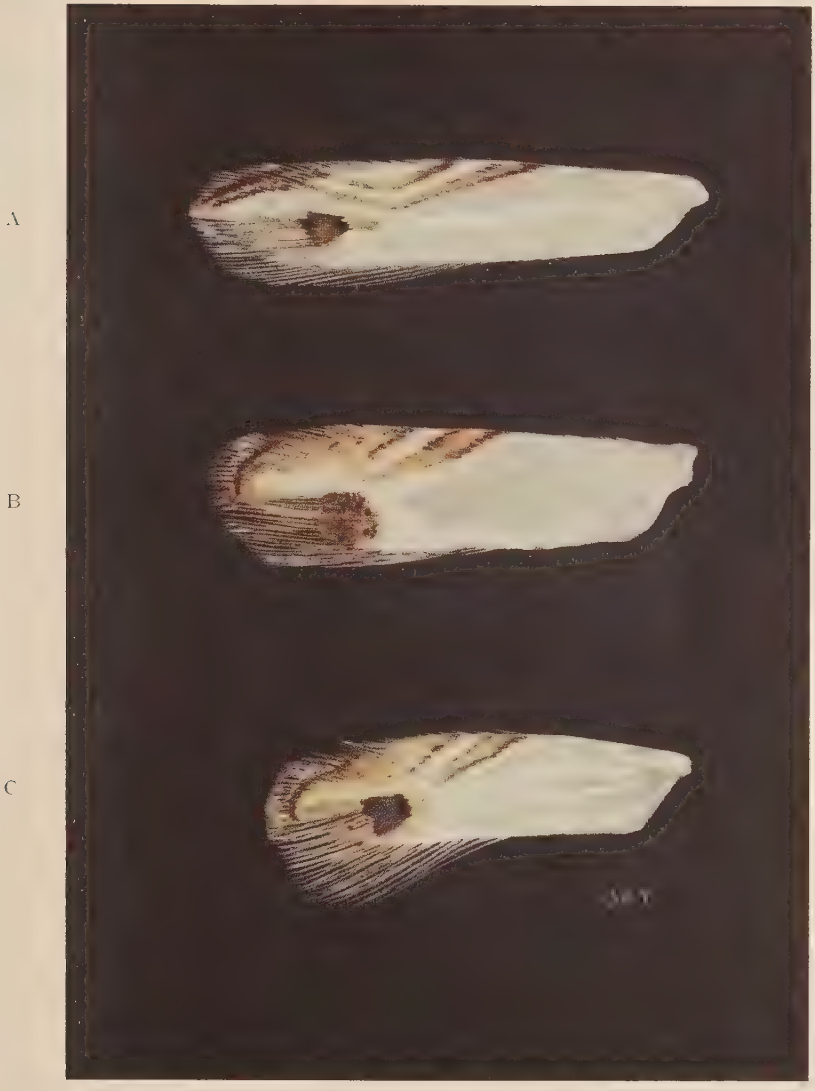

Forewing pattern of
C, [illegible], *Crobylophora staterias*, Meyr.;
B, [illegible], *Leucoptera daricella* (Meyr.);
A, [illegible], *Leucoptera caffeina*, sp.n.

THREE SAWFLIES ATTACKING GUAVA IN BRAZIL (HYMENOPTERA SYMPHYTA).

By Robert B. Benson, M.A.
Department of Entomology, British Museum (Natural History).

Representatives of three species of sawflies attacking guava (*Psidium guajava*, L.) in Brazil, were recently sent for determination by Dr. Louis Pyenson, formerly head of the Entomology Section of the Instituta de Pesquisas Agronomicas, Pernambuco, Brazil. One of these proved to be *Haplostegus epimelas*, Konow (Pergidae, Pergulinae) (*vide* Condé, 1936, Rev. Ent. Sao Paulo, vi, pp. 120–124) ; while the other two belong to new species as follows :—

Acorduleceros megacephalus, sp. nov. (Pergidae, Acordulecerinae).

♂. *Colour* yellow ; wings hyaline with costa, upper part of subcosta, base and centre of stigma and submedian vein yellow ; apex of stigma with upper and lower margins, lower part of subcosta and rest of venation brown.

♀. (Head and forelegs missing.) *Thorax* yellow, with the following parts black : blotch on each side of the pronotum, the middle and side lobes of the mesonotum, the lower half of the mesepisternum and mesepimeron with the whole of the mesosternum, metapleura and legs ; *abdomen* black except for the piceous to yellow 1st tergite and the yellow spot each side of the 2nd tergite ; *wings* hyaline with stigma, costa and venation black.

Length ♂♀ 5 mm. ; forewing 4·5 mm.

♂♀. *Punctation* obsolete. *Pubescence* pale over whole insect except on dorsal part of head and thorax where it is fuscous. *Head* (fig. 1, *a*) not contracted but well-developed behind the eyes, almost parallel-sided ; viewed from above ocelli, length to breadth of head is as about 3 : 5, head behind eye almost as long as length of eye when viewed from above (3 : 4) ; postocellar region not defined ; clypeus acutely excised in the middle of the front margin to the depth of one-third its length ; eyes much farther apart in front than length of an eye (viewed from in front) (7 : 4) ; malar space about two-thirds diameter of front ocellus ; POL : OOL as 2 : 3 ; antenna 6-segmented and shorter than length of head. *Thorax* : front lobes of mesonotum with medial furrow obsolete in posterior half ; praescutal furrows (separating front from side lobes) are, however, well defined behind as well as in front (fig. 1, *a*).

Wings as in *Acorduleceros dorsalis*, Say, except that the stigma is more swollen and produced forward in the ♂ and the anal cell of the forewing is vaguely closed and petiolate through the only partly obsolete anal vein (fig. 1, *b*).

Legs with hind tarsi together only about three-fourths as long as the hind tibia (33 : 45) ; the basitarsus being nearly as long as the rest of the tarsal segments together (15 : 5 : 3 : 2 : 7) ; inner apical tibial spur more than two-thirds as long as basitarsus.

Brazil : Pernambuco. 3 ♂♂ (including holotype), 1 ♀ (allotype) 1937 (*L. Pyenson*, no. 673).

Types in the British Museum.

This species is separated from any previously described *Acorduleceros* at once by the large head behind the eyes, the excised clypeus, the long malar space, the well-developed praescutal furrows dividing the front and side lobes of the mesonotum, and the short tarsal segments. In habits it has an internal stem-boring larva.

I think it is almost certain that a new genus will have to be erected for this remarkable species; I have, however, refrained from doing this myself now, in deference to Mr. O. Condé (Latvia) who has a nearly completed revision of the species of ACORDULECERINAE.

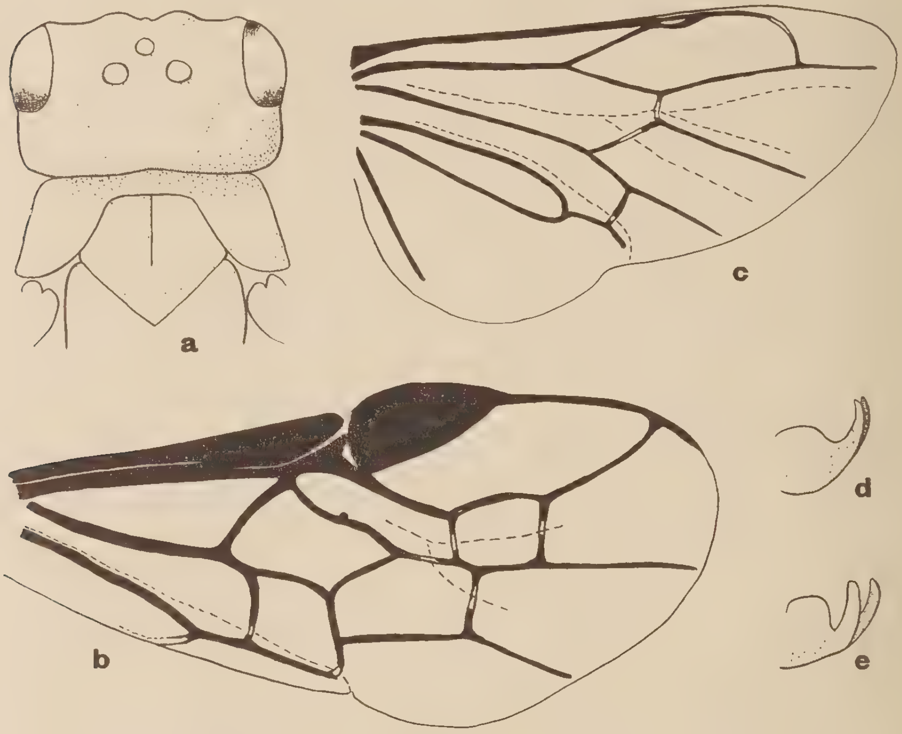

Fig. 1. **a,** Head and front part of mesonotum from above of *Acorduleceros megacephalus,* sp. nov.; **b,** forewing of *A. megacephalus,* sp. nov.; **c,** hindwing of *Metapedias pyensoni,* sp. nov.; **d,** hind tarsal claw in ♂ *M. pyensoni,* sp. nov.; **e,** hind tarsal claw in ♀ *M. pyensoni,* sp. nov.

The second new species belongs to the genus *Metapedias,* Enderlein 1919 (S.B. Ges. naturf. Fr. Berlin, 1919, p. 350) erected for *Blennocampa bicolorata,* Cameron (Mexico) and *B. obscura,* Kirby (Brazil). Since the entire original definition of the genus is concerned with the fact that it differs from *Blennocampa,* Hartig, in having a very large apical cell to the hindwing, a fuller description of the genus is necessary.

Metapedias, Enderlein (re-description).

(Tenthredinidae Blennocampinae, tribe Blennocampini.)

Head strongly contracted behind its large eyes; length of eyes viewed from above 3 or 4 times as long as length of head behind eyes; hind ocelli in front of eye tangent; malar space linear; mouth-parts normal; clypeus slightly convex and either emarginate or slightly produced in front; antenna with two basal segments longer than broad; segment 3 about as long as 4 + 5 or the three apical segments together; on the frons just above the antennal sockets are three pits, one medial (median fovea) and one each side (antennal foveae) in a transverse line; the exact form of these foveae and the punctures and sculpture round them varies between the different species, so does the form of the vertical furrows, bordering the postocellar region laterally.

Wing venation as in *Blennocampa*, Hartig, save for the very large apical cell of the hind wing (about half as long as the radial cell) (fig. 1, **c**). *Legs* stout with hind apical tibial spurs curved and shorter than apical breadth of tibia ; basitarsus usually longer than 3 following tarsal segments together ; hind tarsal segments together shorter than tibia (4 : 5 or 5 : 6) ; claws cleft apically and with a large basal lobe ; the two parts of the cleft apex are side by side at the base, and continue thus almost to the apex on the hind legs of the ♂ (fig. 1, **d**) ; in the ♀, and on the fore and middle legs of the ♂, however, the two parts of the cleft tooth widely diverge from each other towards the apex in lateral view (fig. 1, **e**).

In addition to the species mentioned above, the following species in the British Museum also belong to the genus :—*Blennocampa intermedia*, Cameron (Panama) and *B. subcoerulea*, Cameron (Guatemala), and in addition to these at least three other apparently undescribed species from Central America and Brazil. Furthermore, *Blennocampa rubricollis* (Spinola) Konow, evidently also belongs here, to judge by the original description.

Metapedias pyensoni, sp. nov.

♂♀. *Colour* : Black ; reddish yellow are the whole of the prothorax (notum, pleura, sternum, etc.) and the tegulae. *Wings* smoky, the forewing being darker than the hindwing ; stigma, costa and venation black. *Length* ♀ 6·5–5·5 mm., ♂ 5·5 mm.

Pubescence sparse and more or less infuscate, almost obsolete on mesonotum and dorsum of abdomen.

Punctation : labrum, clypeus, frons, postocellar area and front part of front lobes of mesonotum evenly covered with very fine widely-spaced punctures ; surface between punctures, and whole of temples, mesonotum (except front part of front lobe) and abdomen, entirely smooth and shining.

Head : clypeus slightly emarginate in front ; antenna longer than breadth of head behind eyes (6·5 : 5), segment 3 a little less than 4 + 5 (17 : 19) ; segments 4+5=7+8+9 ; antennal fovea (behind each antenna) of such a size and dimension as to be filled by the convex part of an ocellus inverted ; median fovea of the same diameter but only half as deep as an antennal fovea, with a rounded convexity each side and without any definition behind ; POL=OOL ; POL equal to the distance between an ocellus and the hind margin of the head ; postocellar area raised above temples and broader than long (16 : 9).

Legs with hind basitarsus as long as 3 following and half the 4th following tarsal segments together.

Abdomen with ♀ sawsheath (viewed from above) expanded and rounded at apex where its greatest breadth is about twice that of the narrowed base ; the sides bear straight hairs set at an angle of about 45° to the sheath.

BRAZIL : Pernambuco, 6 ♀♀ (including holotype) and 1 ♂ (allotype), 1937 (*Pyenson*).

Types in British Museum.

This species is separated at once from all other species in the genus known to me by the coloration of the thorax and the sculpture of the frons.

NOTES ON THE BIOLOGY OF THREE TENTHREDINID (HYM.) PESTS OF THE GUAVA.

By Louis Pyenson*, Ph.D.

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*Formerly Head of the Entomology Section of the Instituta de Pesquisas Agronomicas, Pernambuco, Brazil.

(Plate XV.)

For the names of the sawflies I am indebted to Mr. Robert B. Benson of the British Museum (Natural History) (*vide* Benson 1939).

Haplostegus epimelas, Konow (Gregarious Guava Sawfly).

The adults of the Gregarious Guava Sawfly are relatively sluggish insects and can be readily captured on foliage (Pyenson 1938 *b*). They lay their eggs in single rows embedded in the tissue of the tips of young green twigs or along the midribs on the underside of the younger leaves.

In laying their eggs they puncture the tissue with their sawlike ovipositors and deposit an egg in each puncture. The glossy eggs can be readily seen embedded in the tissue. When eggs have been oviposited in the midribs of young leaves, these leaves curl and are readily located on the young shoots. The sawflies lay about 20–40 eggs on a single leaf or stem. These eggs hatch in about 3 days into tiny yellow larvae, which line up side by side and start feeding, beginning at the outer edges of the young tender leaves. They consume in this manner most of the new growth, leaving only the midribs and tougher veins of the leaves. As they grow larger they migrate to older leaves and continue to strip the guava branches of foliage. They appear, however, to prefer the younger foliage and usually migrate from one growing shoot to another, entirely stripping them of foliage. When several such larval colonies are present on a tree they can strip most of the foliage from it. In one locality near the coast in early September, many young guava trees were observed to be almost entirely stripped of foliage by these pests.

The larvae become full-grown in two to three weeks after attaining a length of about 25–30 mm. (fig. 1). They are yellow with brown heads and have a habit of lifting up the posterior ends of their bodies when disturbed. When full-grown the larvae enter the soil to a depth of a few inches and construct pupal cells made of a very thin shiny black silk-like secretion.

Under normal conditions in the rainy season (Pyenson 1938 *a*) the larval and pupal stages in the soil last about 17 days and the total life-cycle a little over a month. However, the larvae may go into a diapause in the pupal cells at the end of the rainy season. Some may remain in this state until late in the next rainy season (June), while some may emerge if there is some rainfall. Larvae which entered the soil in early September (beginning of the dry season) failed to emerge as adults in the normal time. An examination showed them to be full-grown larvae in the pupal cells. However, when the soil was moistened for some time 4 adults emerged 47 days after the larvae entered the soil. The remaining larvae in the pupal cells remained in the same state and were still living 4 months later when some of the pupal cases were dug up and examined. This insect evidently passes the dry season in a state of aestivation as full-grown larvae in pupal cells in the ground. Adults do not appear again until late in the rainy season (June) and breeding continues into the early part of the dry season (September). Two generations were observed during June, July, August and September.

This pest was observed in several localities of the Mata and Litoral Zones (Pyenson 1938 *a*, *b*) and is probably widespread throughout this region.

Acorduleceros megacephalus, Benson (Guava Shoot-boring Sawfly).

The adults are small, yellow, active and hard to catch. The females oviposit in the young tender tips of guava stems. Only one egg is deposited near the end of each growing tip. The eggs hatch in a few days and the young larvae begin burrowing downwards spirally in the tip. The growing tip wilts and finally dies from this injury (figs. 2 and 3). The larvae reach maturity in about 9 days, and usually do not bore more than 5 cm. down the stem in this time. When mature the larvae (about 10 mm. long) bore a hole to the exterior at the base of their tunnels and drop to the soil, which they enter. About 2–3 inches below the surface they form pupal cells of a white cottony-like substance. The total time spent in the soil is 9–17 days, and the life-cycle takes somewhat less than a month.

Injury to guavas from this sawfly was observed at the beginning of the rainy season (early March) and continued far into the dry season (October). Observations on a culture that had entered the soil in the middle of October showed that some adults emerged about 9 days later, but that others continued to remain in the larval stage in the cells. When this same culture was examined early in March, some larvae were found still alive in the pupal cells. Like the Gregarious Sawfly, these insects evidently aestivate in the larval stage in pupal cells in the ground during much of the dry season, and do not emerge as adults until a week or two after the first rains have fallen.

The adults appear to prefer the young tips of the guava watershoots for oviposition, but they have also been observed injuring the growing tips throughout the trees. When this pest is abundant it may severely curtail new growth on the guava trees.

This sawfly was found infesting guava trees throughout the Matta and Litoral Zones of Pernambuco (Pyenson 1938 *a*, *b*).

Metapedias pyensoni, Benson (Guava Sawfly).

The small black adults of the Guava Sawfly may be observed during the rainy season flying about and ovipositing on the upper surfaces of the guava leaves. They lay their blister-like eggs (fig. 4) singly on the older leaves. These eggs are transparent and appear to be glued down on the leaf surface. The eggs hatch in about a week into tiny yellow larvae, which cover themselves with frass and are very hard to detect on the foliage. The larvae feed only on the upper leaf surfaces, leaving brown markings. The sluggish larvae do not remain on one leaf but migrate to others, leaving their characteristic feeding injury. As many as 10 eggs may be laid on a single leaf, but usually few of the larvae reach maturity because of predators, parasites and heavy rains. It takes the larvae about three weeks to become full-grown. The head and mouth-parts of the larvae are hidden by the thorax and cannot be seen from above. This accounts for their peculiar feeding habits. When full-grown (12–15 mm. long) the larvae enter the soil, where they form pupal cells of earth. Under normal conditions 12–20 days elapse from the entrance of the larvae into the soil and the emergence of the adults from the soil. However, early in the dry season some of the larvae in the pupal cells failed to form pupae and emerge in the normal time, but remained as larvae. No observations were made to see how long this diapause would last, but as no larvae were observed from September to April in guava stems, they evidently aestivate in this stage during the dry season like the other two sawflies.

These sawflies were observed throughout the Matta and Litoral Zones of Pernambuco (Pyenson 1938 *a*, *b*).

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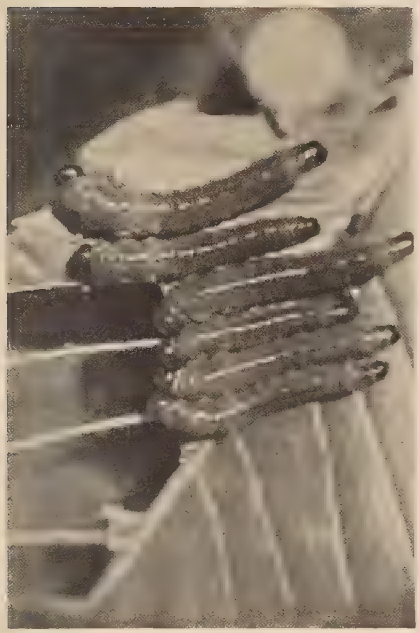

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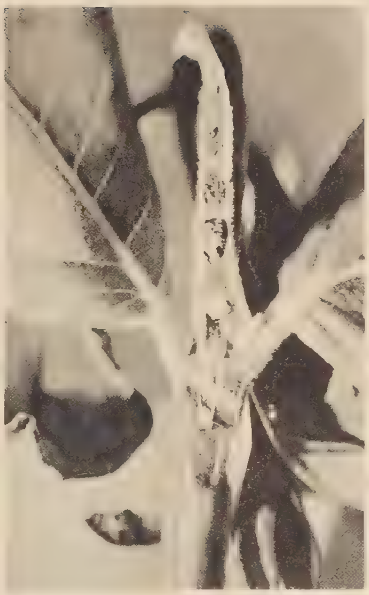

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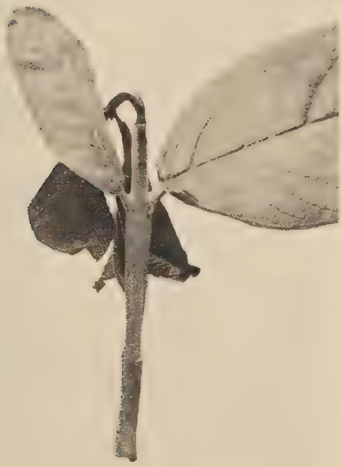

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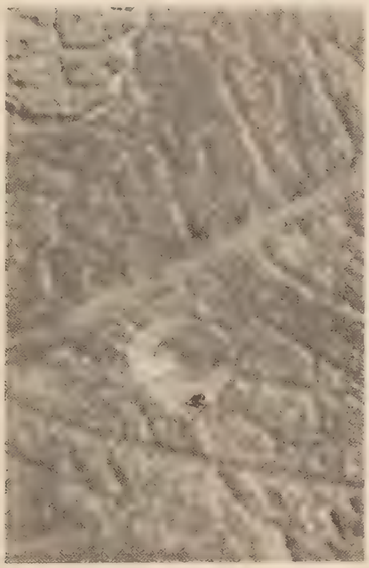

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Fig. 4

Fig. 1. Larvae of gregarious sawfly (*Haplustegus epimelas*, Konow) on Guava leaf.

Fig. 2. Guava shoot injured by sawfly borer (*Acorduleceros megacephalus*, Benson).

Fig. 3. Guava shoot as in Fig. 2 but opened to show larva in situ.

Fig. 4. Egg of surface-feeding sawfly (*Metapedias pyensoni*, Benson).

BIONOMICS OF A GRAPE BORING PLUME MOTH (*OXYPTILUS REGULUS*, MEYR.) IN SOUTH INDIA.

By T. V. Subramaniam, Dip. Agr.

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(Plate XVI.)

Introduction.

The grape vine (*Vitis vinifera*), which is a common fruit crop grown extensively in Mysore, has not been noticed till now to be subject to any very serious insect pests, though one occasionally comes across a Chrysomelid beetle (*Scelodonta strigicollis*, Mot.), stray leaf-eating cockchafers (*Adoretus* spp.), twig-girdling Longicorn beetles (*Sthenias grisator*, F.), and stray scale-insects, which, however, have not done any very serious damage so far ; but recently substantial damage has been caused to the grape vine crop by an insect which appears to be quite a new record—at any rate for S. India. The insect concerned is a species of plume moth (*Oxyptilus regulus*, Meyr.), the larva of which bores into the ripening berries of the grape bunches and causes substantial injury. The grapes grown in the Mysore State belong to a local black variety, the fruits of which have a sub-acid taste and do not therefore fetch good prices at present because of the very large imports of sweet varieties from North India and elsewhere. The serious nature of the damage done by this new pest and the consequent menace to the grape crop, which is one of the oldest of the fruit plants to be raised in the State, and the likelihood of the insect extending its activities to the different varieties of this crop cultivated outside the State, prompted the author to attempt a fairly thorough study of the insect with a view to adopting control measures.

Occurrence and Distribution.

So far as the writer is aware, very few plume moths have been recorded as important crop pests in India. The only one which deserves serious attention is the tur plume moth (*Exelastis atomosa*, Wals.) attacking red gram (*Cajanus indicus*) all over India ; other species known to us as affecting cultivated crops are the bottle gourd and the brinjal plume moths (*Sphenarches caffer*, Z., and *Pterophorus lienigianus* Z.,), which are of minor importance. This new pest of grapes was first noticed in the Government Fruit Garden in the Irwin Canal Farm, Mandya, Mysore District, about 70 miles from Bangalore, in October 1936, and later on reports were received from different localities around Bangalore. The species is known to occur also in Ceylon and northern Australia.

Life-History and Habits.

Egg.

Egg-laying generally takes place during the night, and the eggs are laid singly. They are deposited on the berries, round the fruit-stalks, on the peduncle, and in all spots where the berries in a bunch are contiguous (Plate XVI, fig. 1). The eggs are oval, smooth and shining white when freshly laid, but gradually turn yellowish and become more or less flattened. They hatch in 4 or 5 days and the newly emerged caterpillar does not feed on the egg-shell, as do some other larvae.

Larva (fig. 1).

The newly hatched caterpillar is about 1 mm. long and yellowish with the broad head dark, the prothoracic shield being very pale. The posterior region of the abdomen, which gradually tapers towards the tail end, is of a darker hue. The body surface is sparsely covered with short hairs. As it grows, it assumes a light brown colour dorsally with the head and the interspaces between the segments pale ; the ocelli are shining black and the prothoracic shield brown. Soon after hatching, the larva generally enters the berries adjacent to the fruit-stalk, tunnels through the fleshy pulp and gets at the seeds (Plate XVI, fig. 3). Minute brown pellets of excreta, etc., are thrown out of the entrance hole in the fruits. The larva remains feeding inside the berries from 12 to 13 days and comes out as a full-grown larva for pupation. In cases where the eggs are laid on contiguous berries, the hatching larva is found to bore into the fruits from these situations. The larva has also been noticed to come out of one berry and damage the others close by, so that a number of berries in a bunch are damaged by a single caterpillar. The result is that numerous berries in a bunch are damaged, most of them dropping, and the consequent loss is very substantial. The full-grown caterpillar (fig. 1) is deep chocolate brown, with three dorsal longitudinal, pale yellow interrupted stripes and a broad lateral one on each

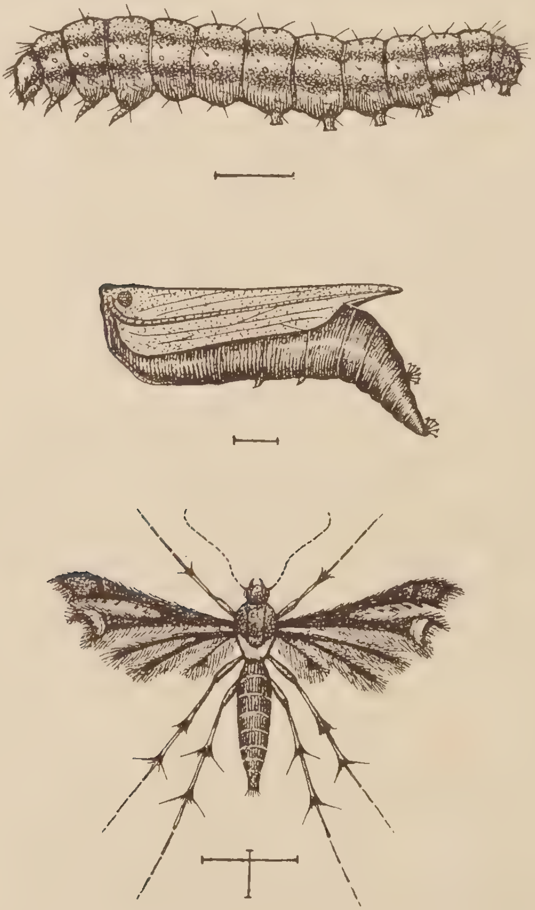

Fig. 1. *Oxyptilus regulus*, Meyr.; larva, pupa and adult.

side. The head and the tail end dorsally are pale yellow, mouth-parts light brown, ocelli shining black, and the prothoracic shield pale, with the anterior margin dark. The larvae attacking ripening berries develop a dark reddish colour. A full-grown caterpillar measures from 8 to 9 mm. long and a little over 1 mm. broad.

Pupa (fig. 1).

Pupation takes place within a day after the full-grown larva comes out of the berries; the pupa is exposed on the peduncle or on the surface of healthy berries, if the infested berries are still attached to the bunch (Plate XVI, fig. 3). The larvae coming out of fallen berries pupate on the weeds and dry leaves found on the soil underneath the plants. The pupa is ashy-coloured at first, but gradually turns to a dark brown, when it is very difficult to distinguish it on the fruit-stalk. Pupation takes place very much as in many other Pterophorid larvae, *viz.*, the caterpillar spins silk on the surface where it pupates and rests on it with the anal prolegs firmly fixed. A distinct bunch of curved hooks form on the anal end and on the underside of the eighth abdominal segment, and with these the pupa gets firmly fixed to the surface with its anterior region free. Two pairs of prominent short, stout, black spines, one on the dorsal surface of each of the second and third abdominal segments are also noticeable. The pupal period lasts 10 days.

The Moth (fig. 1).

The moth is very dark in colour and delicate in build; while at rest, the plumed wings are held at right angles to the body. It is active during the night and rests on the lower surface of leaves and twigs during the day. Mating has not been noted as yet, but the moths begin laying eggs, in captivity, 18 or 19 days after emergence from the pupae. In captivity one generation of insect, from egg-laying to the emergence of the adults, occupies 26 to 28 days (eggs 4 to 5 days, caterpillar 12 to 13 days, pupa 10 days), and the moths live in captivity for about seven weeks. Egg-laying continues for over a month. The moths are found to feed freely on water or very dilute honey. Three generations have been reared in the insectary so far. No alternative food-plants or natural enemies of the pest have been discovered as yet.

Control Trials.

Laboratory trials in dusting healthy grape bunches with pyrethrum powder mixed with wood ashes, as a diluent in various proportions, were carried out. The moths did not lay eggs freely on bunches so treated, but on those dusted with ashes alone innumerable eggs were laid. Fruit bunches having a large number of eggs laid on them were dusted with pyrethrum and ashes in the proportion of 1 to 3 and not a single larva hatching out of these eggs was able to bore into the berries, all such larvae being found dead within 24 hours after having come into contact with the dust. The toxic effect of the pyrethrum placed on the fruits continued for about 14 days from the time of dusting, so that no injury to the fruits was noticed. Many of the moths also which came into contact with the pyrethrum-dusted grape bunches during egg-laying did not survive long. As these trials with pyrethrum have given good promise of control under insectary conditions, it is proposed to carry out field trials in this direction during the coming season, and further detailed investigations are being made on this insect.

The writer expresses his indebtedness to the Director, Imperial Institute of Entomology, London, for kindly identifying the insect for him.

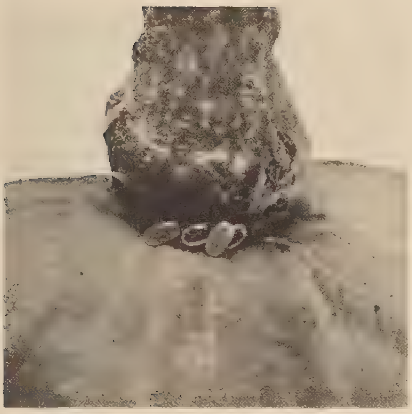

Fig. 1. Eggs at base of fruit stalk.

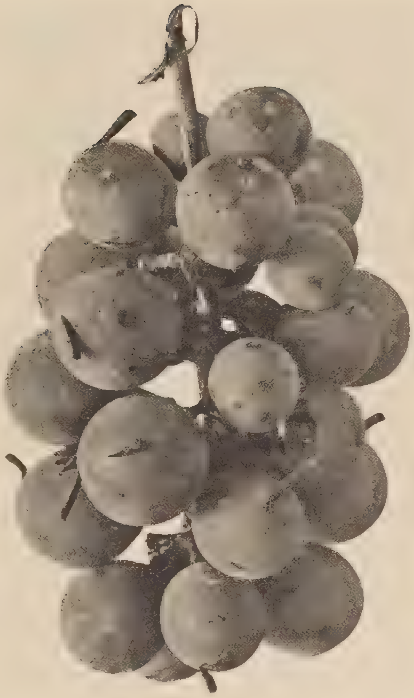

Fig. 2. Pupae attached to healthy berries.

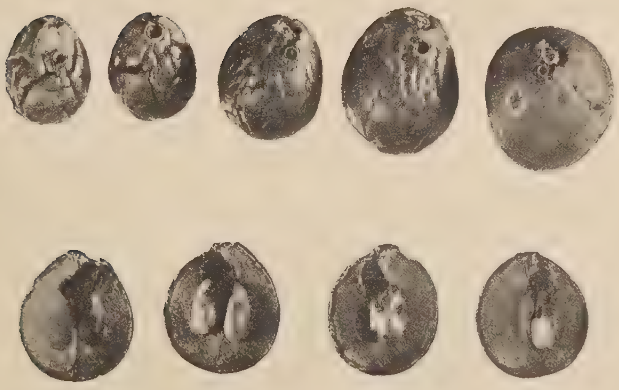

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Fig. 3. Damage to berries caused by larvae.

BIONOMICS OF *OXYPTILUS REGULUS*, MEYR.

OBSERVATIONS ON THE LARVAL DIAPAUSE OF THE PINK BOLLWORM, *PLATYEDRA GOSSYPIELLA*, SAUND.

By F. A. Squire.

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Introduction.

As cotton crops in many parts of the world end either with the onset of winter or of the dry season, it is natural that the larval diapause which becomes more and more conspicuous as the crop ripens should have come to be regarded as an instance of either hibernation or aestivation; yet in the West Indies where the following observations were made, there is no winter, nor does the ripe boll phase of the crop necessarily fall in the dry season. The latter moreover is not one of complete drought but rather dry only by comparison. Indeed in some islands, such as Montserrat and St. Kitts, the crop is harvested in the wet season. Yet long-cycle or resting larvae are regularly found in all of these islands.

As was shown in a previous paper[1] the larval diapause is independent of seasonal or climatic conditions and is caused by food of low moisture content. As the crop ripens and the pest population increases larvae are forced more and more on to older bolls and trophic larvae become more and more common in open bolls within seeds of low moisture content.

Decline in the Moisture Content of Seed after Boll-Split.

In this connexion the moisture content of seeds after boll-split was gone into in St. Vincent with the following results :—

1	day(s) after boll-split	78·5	per cent.
1	,, ,, ,, ,,	61·8	,, ,,
1½	,, ,, ,, ,,	57·6	,, ,,
1½	,, ,, ,, ,,	39·7	,, ,,
2	,, ,, ,, ,,	50·3	,, ,,
2½	,, ,, ,, ,,	20·0	,, ,,
3	,, ,, ,, ,,	20·5	,, ,,
4	,, ,, ,, ,,	31·2	,, ,,
5	,, ,, ,, ,,	10·0	,, ,,
5	,, ,, ,, ,,	39·7	,, ,,
5½	,, ,, ,, ,,	12·9	,, ,,
6	,, ,, ,, ,,	20·9	,, ,,
7	,, ,, ,, ,,	10·6	,, ,,
8	,, ,, ,, ,,	14·3	,, ,,

From fig. 1 constructed on the above data it will be seen that there is a rapid loss of moisture after boll-split.

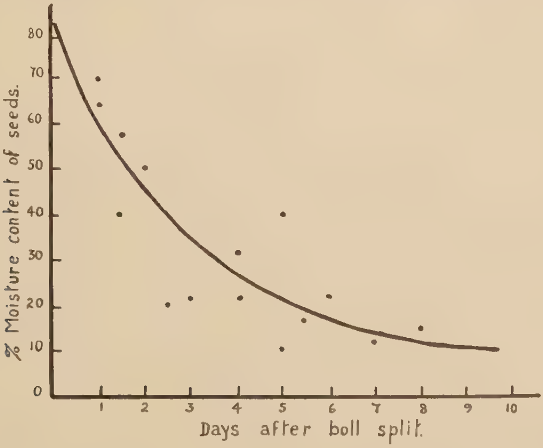

Fig. 1. Decline in moisture content of seeds from boll-split to picking.

The normal duration of the larval stage being approximately 14 days it follows that larvae starting their career within 14 days of boll-split will come more and more under the influence of the decline in seed moisture content according to the date of penetration.

From fig. 1 it is possible to work out the average moisture content of the food consumed in the following way :—

Let 75 per cent. be the moisture content of seeds before boll-split then the following table gives the number of days before boll-split at which penetration took place and the average moisture content of the food consumed by the larva, retardation being left out of account :—

Penetration days before boll-split	Average percentage moisture content of food.
14	75·0
13	73·7
12	71·4
11	68·6
10	65·2
9	61·4
8	57·4
7	53·0
6	48·5
5	43·1
4	39·2
3	34·6
2	29·9

Correlation between Moisture Content of Food and Percentage in Diapause.

This point was investigated in St. Vincent between January–May 1938. The following meteorological table shows the conditions obtaining during that period :—

	Min. temp.	Max. temp.	Rainfall	Relative Humidity 9 a.m. and 3 p.m.	
				Min.	Max.
January	70	85	3·33	59	82
February	67	85	4·67	55	95
March	70	86	3·94	57	90
April	70	87	0·85	56	94

The crop had been planted in September and picking was in full swing. Infested bolls were selected, the full-grown larvae removed and kept under observation and the moisture content of the seed estimated by sample. The larvae were kept in cups with cottonwool covered with muslin. Larvae very readily spin up in cottonwool, those about to pupate in a long sac, while those about to rest curl up in the characteristic manner. The moisture content was determined by heating to a constant weight over a water bath. In the case of young bolls care was taken to count the number of fresh pupae, and in the case of open bolls to exclude larvae which had obviously stopped feeding and spun up some days before. The following figures were obtained :—

Percentage moisture content of food	No. of larvae	Percentage in diapause	Percentage moisture content of food	No. of larvae	Percentage in diapause
78·1 ...	1	0	52 ...	14	35·7
78 ...	24	20	51 ...	12	25
70 ...	26	0	51 ...	2	0
70 ...	40	0	50 ...	7	0
70 ...	10	0	49 ...	20	70
70 ...	16	0	47 ...	1	0
70 ...	6	16·6	46 ...	5	20
69 ...	4	0	45 ...	9	55
68·9 ...	2	0	41 ...	4	25
68·5 ...	7	0	40 ...	35	14·3
68 ...	10	30	37 ...	9	33·3
66 ...	14	35·7	36·3 ...	4	25
65 ...	4	25	36 ...	9	66·6
65 ...	12	0	36 ...	15	13·3
64·4 ...	2	0	35 ...	9	60·6
64 ...	3	0	27 ...	24	50
63 ...	6	33	26 ...	13	69
63 ...	2	50	26 ...	9	55·5
62·7 ...	2	50	26 ...	11	45·5
62·1 ...	3	0	25 ...	8	12·5
60 ...	12	55	24 ...	6	66·6
60 ...	6	33·3	22·4 ...	4	0
59 ...	11	9·1	20 ...	11	45·5
58 ...	19	21	20 ...	11	27·2
58 ...	8	50	20 ...	6	66·6
57 ...	7	43	19·2 ...	12	66·6
57 ...	18	27·7	15 ...	9	77·7
55 ...	19	63	13·8 ...	6	66·6
55 ...	7	14·3	8·6 ...	11	46·4
54 ...	20	45	7·6 ...	9	66·6
53 ...	8	12·5	7 ...	13	46·1

Plotting these figures, from the dot diagram (fig. 2) it will be seen that there is a suggestion of a negative correlation. These results were analysed statistically according to Fisher's method, and r equalled 0·397. The significance of the observed correlation was worked out by Fisher's method $n=54$ and $t=3{\cdot}178$ which according to the table of "t" is highly significant.

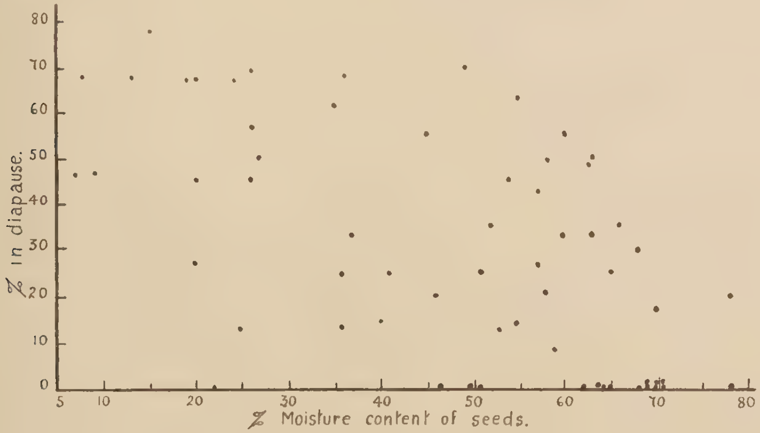

Fig. 2. Correlation between the percentage of larvae in diapause and the percentage moisture content of food.

Condensing and grouping them according to the percentage moisture content, the following figures are arrived at :—

Percentage moisture content	Number of larvae	Percentage in diapause
70–80	123	5·2
60–70	89	20·8
50–60	152	26·6
40–50	74	30·7
30–40	46	39·8
20–30	103	43·8
0–20	60	62·0

It will be seen that under the stated conditions of temperature and humidity food containing 0–20 per cent. of moisture causes 62·0 per cent. of the larvae to go into diapause while food of 70–80 per cent. moisture content gives rise mostly to short-cycle forms.

Correlation between Ripe/Green Boll Ratio and Percentage of Immature Larvae in Bolls.

Tagged bolls from a given plot were examined on the day of boll-split and the infesting larvae divided into their instars, the fourth or last instar being divided into full-fed and not full-fed. From these data the percentage of immature larvae on successive days was ascertained. At the same time the ripe/green boll ratio for the plot was ascertained by counts, the results being shown in the accompanying graph (fig. 3).

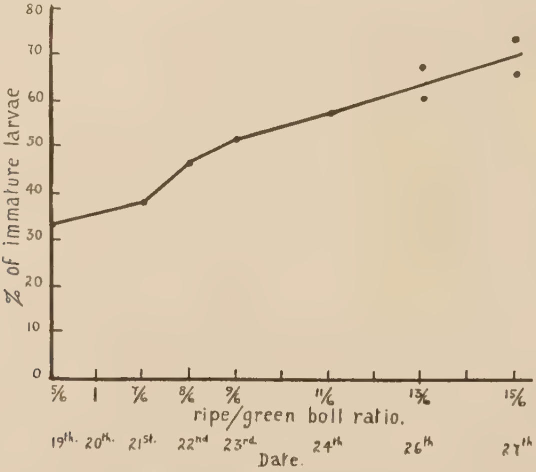

Fig. 3. Correlation between the ripe/green boll ratio and the percentage of immature larvae present in bolls on day of boll-split.

It will be seen from this figure that the percentage of immature larvae increases with the ripe/green boll ratio.

Owing to retardation and mortality caused by dry food the number of larvae continuing to feed after boll-split tails off rapidly so that in any sample of resting larvae the number feeding on successive days after boll-split is distributed in the form of a Poisson series.

Termination of Diapause by Wetting.

Ten Montserrat resting larvae which had been in the resting stage some six weeks were allowed to spin up in cottonwool in each of twelve glass slides bound with passepartout which was punctured to admit air. Enough water to saturate the cottonwool was injected with a hypodermic syringe into six of these slides which were then stood on end to drain off. The results are given below :—

Date and Remarks	Treated						Controls					
	1	2	3	4	5	6	1	2	3	4	5	6
Dec. 11 treated lot wet.												
,, 20 pupated	1	1	1	—	—	1	—	—	—	—	—	—
,, 22 ,, ...	1	—	—	—	2	—	—	—	—	—	—	—
,, 23 ,, ...	—	1	—	—	1	1	—	—	—	—	—	—
,, 28 ,, ...	—	1	1	—	—	1	—	1	—	1	—	—
,, 29 treated lot wet again.												
,, 31 pupated	—	1	—	—	—	—	—	—	—	—	—	—
Jan. 4 ,, ...	—	1	—	—	—	—	—	—	—	—	—	—
,, 5 ,, ...	1	1	—	—	—	—	—	—	—	—	—	—
,, 8 ,, ...	—	1	—	—	—	—	—	—	—	—	—	—
,, 9 ,, ...	2	—	—	1	1	—	—	—	—	—	—	—
,, 10 ,, ...	1	—	1	1	—	—	—	—	—	—	—	—
,, 11 ,, ...	—	—	—	1	—	1	—	—	—	—	—	—
,, 12 ,, ...	—	—	—	1	—	—	—	—	—	—	—	—
,, 17 ,, ...	—	1	—	1	—	—	—	—	—	—	—	—
,, 29 ,, ...	—	—	—	2	—	—	—	—	—	—	—	—
Pupated	6	8	3	7	4	4	—	1	—	—	1	—
Mortality of larvae	4	1	4	3	5	3	1	4	2	1	0	0
Percentage of survivors pupated	100	88·8	50	100	80	57·1	0	16·6	0	0	11·1	0

It will be seen that pupation took place in two waves at roughly 6–9 days after each wetting. The percentage of surviving larvae pupated up to the end of January was 80 in the treated as against 3·8 in the controls.

The Termination of Diapause at Different Humidities.

Twelve vials each containing ten resting larvae spun up in dry cottonwool were placed in desiccators, half at 90 per cent. R.H. and half at 60 per cent. R.H. These air humidities were procured by means of solutions of potassium hydroxide made up according to Paranjpe's tables quoted by Buxton[2]. The experiment was repeated for different periods, and the air temperatures during the experiments fluctuated between 67°F. min. and 85°F. max.

The results are presented graphically (fig. 4). The six pairs of percentages were examined by Fisher's method for the Comparison of Means and the differences in every case proved to be significant.

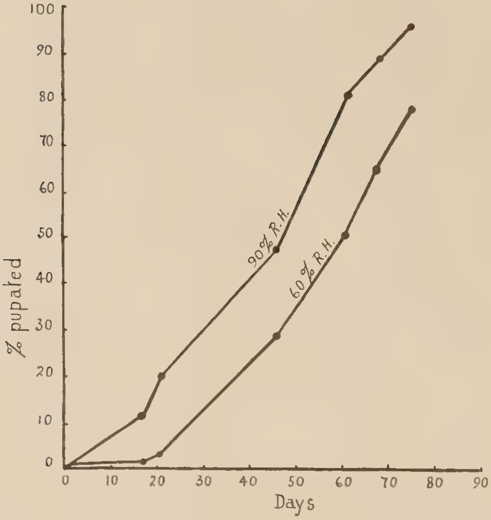

Fig. 4. Termination of diapause at different humidities.

Duration of the Diapause.

The duration of diapause is important in connection with the close season; yet very little is known about it. There are the well-known records of Gough, Busck, and Wilcocks, showing that occasional larvae can survive for two years or more.

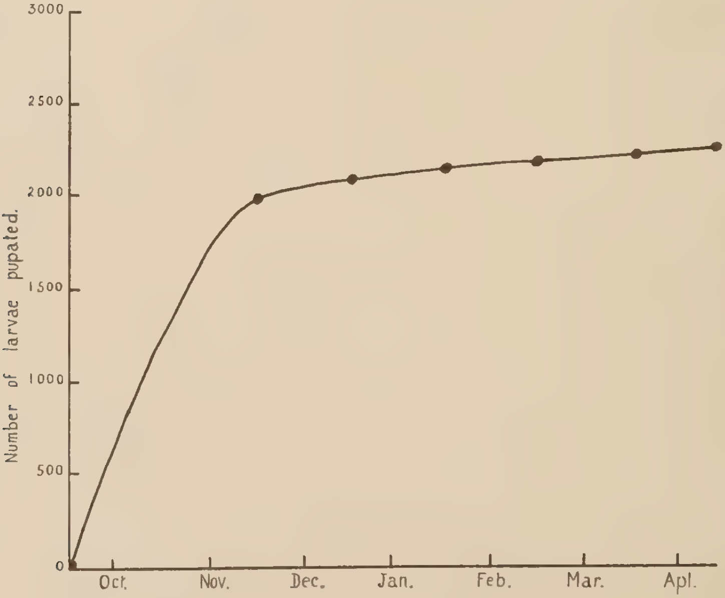

Fig. 5. Rate of pupation of resting larvae.

From about the middle of October to the middle of November 1937, 3,000 resting larvae were collected in Montserrat. That was the last month of the crop and double seeds in open bolls were plentiful. The rainfall at the Grove for October was 5·64, that for November 5·13, the temperature ranged from 70 to 90°F. and the humidity from 54 to 70 per cent. R.H. These larvae were removed from the double seeds and allowed to spin up in cottonwool in glass slides where they could be easily observed. The results are shown in fig. 5. The conditions in which these larvae were kept resemble those which they would find in dilapidated ginneries, cotton houses and peasant abodes. It will be seen that nearly one-third was still in diapause at the end of April; so that clearly the question of sanitation must be tackled.

Practical Implications.

The survival of resting larvae in the soil and in cotton residues in the field is favoured by dry conditions. Where practicable, therefore, the close season should fall in wet months. Furthermore, owing to their sheltered habitat resting larvae in buildings are able to survive the close season, so that it is important to insist on sanitary conditions in ginneries and cotton houses as well as in peasant abodes in which cotton is kept and sorted.

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FURTHER NOTES ON THE ECOLOGY AND CONTROL OF PINE BEETLES IN GREAT BRITAIN.

By H. S. Hanson.

Farnham House Laboratory, Imperial Institute of Entomology.

(Plates XVII, XVIII, XIX.)

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1. Introduction.

The following is an account of the continuation of experiments and observations carried out in connexion with an investigation into the ecology and control of pine beetles, with special reference to *Myelophilus piniperda* and *M. minor*.

The work was undertaken by the Imperial Institute of Entomology on behalf of the Forestry Commission. An account of the economic status of the insects and the nature of the damage they cause, has already been published, together with a description of the earlier experiments and the results obtained. The previous work was carried out almost entirely in the New Forest, but during the last two years the experiments have been extended on a larger scale and under a greater variety of forest conditions in various parts of Great Britain. The work afforded considerable opportunities for studying the distribution of the various species of bark-beetles and their parasites and predators. Certain species which a few years ago were considered to be rare and very local in distribution have been found to be fairly numerous and widely distributed. Other species, of which individual specimens had been recorded, are in reality well established as breeding species. Several species of parasites have been found which had not previously been recorded in Britain.

Various species of bark-beetles are constantly being introduced from the Continent of Europe, and the steadily increasing area of coniferous forest in this country will doubtless provide greater facilities for these aliens to become established as resident breeding species. Greater attention to the study of forest entomology is therefore necessary.

2. The Nature and Scope of the Investigation.

The investigation was commenced in 1933 and was undertaken in order to determine the nature and extent of the damage actually caused by the reduction in value of pine crops as a result of the attack of pine beetles ; to study the conditions which favour the development of the pine beetles and enable the population in any particular locality to become sufficiently numerous to cause damage to the crop ; also to determine what conditions favour or hinder the development of the parasite and predator populations, the ultimate object being the control of the pine beetle populations.

The control of pine beetles and other injurious insects has occupied the attention of forest entomologists in various parts of the world for many years and much useful work has been done, particularly in European countries, in drawing up rules and control measures, but these control measures are almost entirely directed towards the destruction of insects which are actually found to be doing damage, and the general tendency is to wait until outbreaks occur and then apply the prescribed remedy. This appears to be a perfectly sound course of action, particularly when we consider that the control measures are expensive to put into operation, and it does seem that expenditure in the form of control measures can only be justified by the actual results obtained in the form of injurious insects destroyed. The value of the results thus obtained must, however, be offset by the amount of damage which has already been caused by the insects, and the longer the control measures are delayed the greater will be the amount of damage, consequently the greater the reduction in value of the results of the control measures. On the other hand, the earlier the control measures are put into operation the less will be the amount of damage done to the crop and the greater the value of the results obtained. It will be seen, therefore, that it is of greater importance to prevent insects from doing damage, than to destroy the insects after the damage has been done. Consequently, it is of infinitely greater importance to prevent an outbreak of pine beetles than to collect and destroy successfully immense numbers of insects after the crop had been devastated.

There is an abundance of evidence to show that damage by pine beetles is widespread, every infestation leaves its mark on the crop where it occurs, and the heavier the infestation the greater the extent of the damage. There is no longer any doubt as to whether infestations will arise if conditions are favourable. We know that an infestation is inevitable if breeding facilities are available for the beetles, and we also know that the magnitude and importance of the infestation depends on the extent of the suitable breeding facilities and the extent and value of the crop subject to their attack. The only entirely successful way to combat the insects is to prevent their excessive increase and keep the pine beetle population below the level at which damage to the crop becomes of economic importance. It is, however, of the utmost importance that no useless expenditure should be incurred in taking precautionary measures which may be quite unnecessary, and many of the experiments carried out during the investigation were for the purpose of ascertaining how unnecessary expenditure can be avoided.

As the control of bark-beetle populations was the primary reason for and the ultimate object of the investigation, the methods adopted, as regards both experiments and collection of data, were designed to facilitate the unbiased evaluation of the various factors which have a direct or indirect influence on the existence, distribution, increase and survival, or failure of the insects to survive, under various combinations of ecological conditions, as it is only by means of the detailed study of each combination of factors which affect the various types of organisms that we can arrive at an understanding of biological problems.

Hitherto, biological control methods have been mainly directed to the control of insects that have been introduced into countries in which they did not previously exist, and the basic assumption underlying the method is that the insects increase in the new environment because of the absence of the natural enemies which normally controlled their rate of increase in the country from which they came.

Nevertheless, it is not quite true that insects are, in all cases, completely controlled by their natural enemies in the country of origin. The object of the present investigation was to ascertain how the various factors operate in controlling insect populations and to find out, if possible, how the effects of these factors can be intensified so as to control indigenous insects more effectively. The regulation of population densities is the central problem of the biological control of insects and most of the differences of opinion as to the importance of the various factors of control appear to arise through neglect to appreciate the fact that every factor plays its particular part, directly or indirectly, in determining not only at what density the population may exist, but even the possibility of existence. As B. P. Uvarov (1931, p. 5) has pointed out " The ecological conception of economic entomology consists in the recognition of the injurious insect as an integral part, and even as a product, of its environment."

The chief difference between the method adopted in the present investigation and the methods generally adopted lies in the fact that in the present case an attempt has been made to analyse the natural environment instead of studying the insects under controlled laboratory conditions, and also, what is perhaps more important, the host plant was made the centre of the problem. Special attention has throughout been paid to the ecology of the tree and its silvicultural requirements ; the writer is convinced that this is absolutely essential if a correct solution is to be found for the control of forest insects. The importance of this has recently been pointed out by J. W. Munro (1938) who writes " That it should be ignored is the more surprising if we remember that it is the plant host and its protection that is the reason for the whole discussion." Every effort has been made to ascertain how the various ecological factors interact, both as regards the development of the host plant and the insects that attack it, in order to understand how the fundamental biological principles operate in the regulation of the density of insect populations in general and those of pine beetles in particular. Some of the data collected have a more direct bearing on the control of other forest insects, but no attempt will be made to discuss these in detail in the present paper, as in most cases further investigation will be necessary on somewhat different lines.

3. Results of recent Experiments.

(1) *Thinning Experiments.*

During the last twenty years many thousand acres of pine plantations have been laid down in Britain. Many of these areas are now approaching the stage at which they require to be thinned and it will be necessary to repeat the thinning process at intervals of a few years. Within the next few years the thinning programme will amount to tens of thousands of acres each year.

In recent years advocates of clean forestry have emphasized the necessity for keeping the forest floor clear of all material in which injurious insects may breed. This has led to the belief that it is necessary to collect and burn all unsaleable material which remains when a thinning has been carried out and the saleable produce has been removed. On some private estates this clearing process is religiously carried out, but, generally, the collecting and burning is done after the material has ceased to be suitable for the breeding purposes of pine beetles, and often while it contains large numbers of parasite larvae and predators. In many cases the material is collected into heaps and burned in convenient spots where blanks occur within the stand, and the bark on a circle of trees surrounding each spot becomes scorched. This process has often been witnessed by the writer, and these circles of trees with scorched bark may be seen in pine woods on many private estates where so-called clean forestry is practised. The destruction caused by scorching the bark of the trees could be avoided by carrying the material out to the nearest ride to be burned, but this would materially add to the cost. The really important point is whether it is necessary to collect and burn this material. It is recognised that the limitation of the increase in the pine beetle population is largely dependent on the restriction of the suitable breeding facilities, but no useful purpose can be served by the expenditure of money on the destruction of material which is unsuitable for breeding purposes or material which, although to some extent suitable for breeding purposes, does not form a menace because it affords greater facilities for the development of the parasite and predator population. The cost of collecting and destroying the material sometimes runs into several pounds per acre, but even at a cost of only £1 per acre, the collection and destruction of all unsaleable material produced during the thinning of pine plantations would within the next few years involve an expenditure of several thousand pounds each year in the Forestry Commission's areas alone. Some of the experiments were, therefore, designed to ascertain whether this expenditure is necessary. The earlier experiments have been described and the results published in a previous paper (Hanson, 1937) but for convenience the main points will be summarised here.

For the purpose of the experiments two unthinned plantations were selected in the New Forest in 1933. One area was in Lodge Hill Enclosure and the crop was 20 years of age ; the other was in Buskett's Enclosure and was 30 years of age. In both cases the thinnings were marked and carried out by the forest staff and represent the normal treatment, except that the thinnings were carried out in strips one chain in width, four chains being left unthinned between each thinned strip. Each year every fifth strip was thinned. In the first year, the first, sixth, eleventh, etc. ; in the second year, the second, seventh, twelfth, etc. ; in the third year, the third, eighth, thirteenth, etc., strips were thinned. During the first season the whole of the thinnings were left lying as they fell, so as to give rise to the normal bark-beetle infestation for the maximum amount of material in each age class, it being anticipated that the density of the infestation would vary according to the quantity and quality of the material produced by the thinnings in each area ; the density of the infestations could then be assessed and a comparison made between the infestations in the thinned and unthinned portions, and also between that of each crop.

For the purpose of collecting data, a sample plot one chain by one chain was marked off with white paint in each of the thinned strips, and another sample plot of the same size in each of the unthinned areas, each of the latter sample plots being separated from the thinned strips by a strip of the unthinned portion.

In order to arrive at an estimate of the density of the infestation throughout the area, the pine shoots which fell as a result of the pine beetle attack were collected in all the sample plots, both in the thinned and unthinned areas. This does not give the actual number of the pine beetles, but it does give a fairly accurate estimate of the density of the infestation in terms of damage done by the beetles which emerged from the breeding material, as although *Myelophilus* will travel considerable distances in order to concentrate on suitable breeding material, they do not, on emerging as adults, immediately disperse throughout the forest in search of suitable food material, but attack the shoots at the apex of the crown of the trees in their immediate vicinity. A few beetles did attack trees just outside the thinned strips, but the majority attacked trees within the strips in which they were bred. This is clearly shown by the number and position of the fallen pine shoots.

The method adopted in the collection of shoots in the experimental plots was as follows : Two rows of trees were taken at a time, running in the direction of the long axis of the strip and a line was run out to mark the boundary. The shoots lying between and on each side of these rows of trees were collected, counted and booked. As the rows of trees were 4 ft. apart. this gave 8 sets of figures for each sample plot.

In order to find out the rate of fall-off, in the number of shoots on each side of the thinned strips, the shoots were collected in four double rows in the unthinned portion of the plantation bordering each side of the sample plots. Collections were made at intervals during the autumn and winter, the last collection being made in March just before the shoots began to fall as a result of spring feeding. The figures were plotted to show a curve representing a section one chain wide, running across the thinned strip and including half a chain of the unthinned area on each side. The average density of the shoots within the thinned strips in the Lodge Hill experiment in 1933 was 18,380 per acre, falling away on each side to the level of the density found in the sample plots in the unthinned area which was 1,725 shoots per acre.

In the Buskett's Enclosure experiment in 1933, the average density of the fallen shoots collected in the thinned portion was 25,610 per acre, falling to 1,370 shoots per acre in the unthinned portions. In both cases the figures represent the effects of leaving the whole of the thinnings on the ground.

An examination of the material in the thinned strips showed that 73 per cent. of the *Myelophilus* galleries were in the rough-barked material at the base of the poles.

During 1934 the thinnings were made in the second series of strips in each experimental area, and in order to ascertain what would be the effects of leaving only thin, smooth-barked material on the ground in the thinned strips, the thick, rough-barked material was eliminated by cutting off a 6 ft. length from the base of each pole. The fallen shoots were collected as in the previous year and the results were as follows.

In the Lodge Hill area the number of shoots in the thinned strip was actually less than in the unthinned area. The average number in the thinned strips was 1,690 per acre, as compared with 2,975 per acre in the unthinned areas.

In the Buskett's area the average number of shoots in the thinned strips was 4,240 per acre as compared with 950 per acre in the unthinned areas.

The difference in density of the infestations in the two areas in 1934 is accounted for by the difference in the quantity of breeding material. In Lodge Hill the superficial area of bark was 2,756 sq. ft. per acre as compared with 3,475 sq. ft. per acre in Buskett's.

In order to be certain that the reduction in the density of the infestation was actually the result of the reduction of breeding facilities and not due to seasonal fluctuation, the method of treatment adopted in 1935 was to cut off a 6 ft. length from the base of each pole as in the previous year, but the 6 ft. lengths from one thinned strip were transferred to another strip so as to provide double the quantity of thick-barked material in the latter strip and none in the former. Sample plots were marked out and shoots collected as in the previous years. The results showed that the desired object had been achieved. The average density within the augmented strip at Lodge Hill was 76,520 shoots per acre as compared with an average of 3,870 per acre in the unthinned area. The average density in the augmented strip in Buskett's was 75,020 shoots per acre as compared with 2,190 per acre in the unthinned area. In both Lodge Hill and Buskett's experimental areas, in the strips from which the rough-barked material had been removed, the infestations were only slightly higher than in the thinned strips, which had been treated in the same way during 1934, so the results of the thinning experiment in 1935 showed quite clearly that the intensity of each infestation was directly associated with the quantity and quality of the breeding material available and was not due to seasonal fluctuations. The figures for the three years experiments in each area are shown in Table I.

Although the great majority of the beetles attacked the trees within the thinned strips, a small proportion of the beetles attacked trees outside but in the immediate vicinity of the strips, as is shown by the collection of shoots in the areas bordering on the thinned strips. The effects of this dispersion may actually subject each strip to three infestations: a slight one arising from the thinning of the adjoining strip in the previous year; the main infestation during the year in which the thinning takes place within the strip; another slight infestation during the following year when the next strip is thinned, since the rotation in the thinning operations cause an overlap in the distribution of the beetle infestations arising from each year's thinning. This outspread or overflow is only important when the infestation within a thinned strip is heavy; it increases with the intensity of each infestation, decreases as the intensity of the infestations diminishes, and ceases to be of importance if an infestation is low, as in the case of the Lodge Hill experiment in 1934 when the infestation within the thinned strip was actually lower than in the unthinned area.

TABLE I.

Year	Method of treatment	No. of fallen shoots per acre in	
		Thinned strips	Unthinned areas
	Lodge Hill Experimental Area		
1933	All material left lying in the thinned strips	18,320	1,725
1934	Thick-barked material removed; only thin-barked material left	1,690	2,975
1935	Twice normal quantity of thick-barked material present	76,520	3,870
	Buskett's Experimental Area		
1933	All material left lying in the thinned strips	25,610	1,370
1934	Thick-barked material removed; only thin-barked material left	4,240	950
1935	Twice normal quantity of thick-barked material present	75,020	2,190

The experiments show quite clearly that, while a large infestation may result from leaving the whole of the material lying on the ground during the breeding season when normal thinnings are being carried out, there is no risk of a heavy infestation when only the thin-barked material of small diameter is left lying on the ground when thinning young pine plantations in strips of one chain in width with a distance of 4 chains between the thinned strips, and that the danger of heavy infestations is increased in proportion to the amount of suitable breeding material that is left in the area. The heaviest infestation in 1934 resulted in less than one fallen shoot per square yard, throughout the autumn and winter. This represents an average of only 5 shoots from each tree left standing in the thinned strip, and it must be remembered that much of the material which was left lying for experimental purposes was of a marketable size, being over 3 inches in diameter, and would normally be removed. Consequently, the results of leaving only material under 3 inches in diameter would result in a much lighter infestation than that which arose in the thinned strips in the 1934 experiments.

It will readily be appreciated that leaving the slash and small diameter, thin-barked, unsaleable material on the ground in thinning plantations, will result in an immense annual saving in expenditure, when it is remembered that, in the aggregate, tens of thousands of acres will have to be thinned each year.

The saving in expenditure is not the only commendable feature. An examination showed that the parasite population in this material may be very high. From a sample plot 1/10th of an acre, 6,461 parasite larvae were collected ; this represents a population of 64,610 parasites per acre, and they represent the destruction of that number of pine beetle larvae. A very large predator population is also present. It will be seen, therefore, that the destruction of the unsaleable material not only incurs unnecessary expenditure, but also results in the destruction of the valuable parasite and predator population. Removal of the material also prevents the accumulation of litter which would improve the productivity of the forest soil.

The method of thinning in strips one chain in width was adopted entirely in order to facilitate the collection of data ; it must not be supposed that this method is considered to have any value for practical application. It would be extremely inconvenient to put into practice when thinning is being carried out on a large scale, in fact it is not considered either necessary or desirable that thinning should be carried out in strips under ordinary forestry conditions.

One advantage of leaving the slash and small diameter material on the ground is that it helps to maintain a permanent population of parasites and predators, but thinning in strips is not essential for this purpose. Observations have shown that there is a redistribution of the parasite and predator population each year, and the normal practice of thinning the whole of a compartment or section of the forest in one season would not seriously hinder this redistribution. The normal arrangements of felling series and working circles would provide all the necessary facilities.

It must be remembered that although the results of the experiments show that there is no risk of a serious infestation arising when small diameter, smooth-barked material is left lying on the ground, when thinnings are carried out in strips one chain in width four chains apart, these results provide no evidence as to the intensity of the infestation which would arise when the whole of a compartment is thinned simultaneously. Although the same amount of similar material would be left per acre throughout the area, the effect would not be an increase of five times the amount of breeding material within the compartment, since a certain amount of suitable breeding material exists in the unthinned area between the thinned strips, and a proportion of the parent population does actually breed in these standing poles. The simultaneous thinning would, however, precipitate a considerable increase in the amount of breeding material, and the possible results are in several directions. The parent population would be distributed over a much greater amount of breeding material and the progeny would be distributed more evenly throughout the compartment, with a possible reduction in the level of the infestation. On the other hand, the wider distribution of the parent population might have the effect of reducing a certain amount of mortality which would have taken place owing to overcrowding among the broods of the beetles which would have been attracted by the standing suppressed trees in the unthinned area ; this would tend to increase the total population of the progeny. There is also the possibility that the increased amount of breeding material might attract a larger parent population from the surrounding forest, in which case the general level of the infestation within the thinned compartment would be correspondingly increased, unless a point was reached when the factor of overcrowding again came into operation among the developing broods. However, as the available material within the thinned strips in the 1934 experiments was not heavily attacked for breeding purposes, and was evidently less attractive than the unhealthy poles standing in the unthinned area, there seemed to be little probability that an increase in the amount of this unattractive material would result in the attraction of beetles from the surrounding forest, or that the simultaneous thinning of the whole of a compartment would result in a large increase in the intensity of the resulting infestation.

In order to obtain more substantial evidence on these points, it was considered necessary to extend the scope of the experiments. For this purpose, larger areas were required, and as the necessary areas of suitable plantations were not available in the New Forest, these areas had to be found in other parts of the country. In the meantime the experimental areas in Lodge Hill and Buskett's Enclosures in the New Forest were utilised during 1936 for other experiments which will be described later.

The object of the thinning experiments carried out in 1937 was to ascertain whether the simultaneous thinning of the whole of a compartment would result in a much heavier infestation than when a similar thinning is carried out in strips one chain in width with four chains of unthinned area between the thinned strips. In order to make a fair comparison it was considered necessary to include both methods within the same experimental areas so that the conditions as to the crop would be the same. In case the results did differ considerably, it was thought to be desirable that there should be an intermediate stage for further comparison. The experiments were therefore laid out as follows :—

Each area to be thinned in strips of one chain, two and a half chains and five chains in width, the minimum length of the strips to be five chains, the widest strip to represent conditions where thinning is carried out simultaneously throughout a compartment. The areas to be selected and thinnings carried out before the end of March.

Sample plots to be marked out in each of the thinned strips and in each of the intermediate un-thinned areas during the summer. The fallen shoots to be collected in these sample plots during the autumn and winter of 1937–38.

Three experimental areas were selected. The first was in a 16-year-old Scots pine plantation at Swaffham in Norfolk. This area was selected as being representative of the conditions which exist in the extensive pine plantations which have been established by the Forestry Commission during recent years in the eastern counties of England.

The second was in a 43-year-old Scots pine plantation in Delamere Forest in Cheshire. This area was selected as being representative of the older established plantations in various parts of England which are growning at low elevation under conditions resulting in fairly rapid growth necessitating early and frequent thinning, and which have previously been thinned, but were neglected during the early stages of development.

The third was in a 48-year-old Scots pine plantation on the Glendye Estate in north-east Scotland. This area was selected as being representative of the older established plantations in various parts of the north-east and north of Scotland which are growing at fairly high elevation under conditions resulting in slow growth which does not necessitate early thinning, and which have not previously been thinned. The conditions existing in each of the three areas were entirely different, and the method of treatment in each case was adapted to suit the requirements of the crop and the general situation, and was based on the procedure which would normally be applicable in similar circumstances both as regards the type of crop and the disposal of the material which would under ordinary circumstances be marketable. The forester in charge of each area was consulted on these points, and in each case the thinning was marked and carried out by the forester in charge and his staff.

The data were collected in each case with reference to the density of the pine beetle infestation in relation to the type and quantity of unsaleable material which was left on the ground, instead of being collected and destroyed. The ultimate object being to ascertain whether continuous thinning throughout a compartment during a single season produced a heavier pine beetle infestation than occurs when the thinning is carried out in strips as in the previous experiments.

Thinning Experiments in the Eastern Counties.—The pine areas in the eastern counties of England were established on land which was formerly used for agriculture, but had gradually become impoverished and had fallen out of cultivation as being unprofitable for agricultural crops. Large areas had reverted to waste stretches of Breckland. Although at very low elevation, these areas were very exposed and windswept, and the low annual rainfall helped to complete a combination of ecological factors which presented little choice in the selection of species of trees suitable for planting over such a large area without running serious risk of great financial loss, and complete failure from a silvicultural standpoint. Pines were obviously the trees most suitable for the purpose. Scots pine is one of the least exacting as to soil requirements and one of the most accommodating as to climatic conditions, and is undoubtedly one of the best species to plant on a large scale on poor land not previously afforested. Because of this combination of special qualifications, Scots pine was the tree most extensively used.

On account of economy in planting costs, the young trees were spaced rather wide apart and in view of subsequent developments it would appear that this was false economy. Once the trees reached the thicket stage the soil conditions rapidly improved in quality and although the trees suffered heavily from attacks of the pine-shoot moth, the plantations as a whole have made excellent growth and Scots pine has demonstrated that a slightly increased expenditure on the establishment of the crop in the form of closer planting would not have been misplaced confidence. The heavy attack of pine-shoot moth has resulted in many of the trees becoming badly deformed as regards both stem and crown, and the rapid development of the trees in the pole stage has rendered a special form of early thinning necessary in order to eliminate the badly shaped trees before they spoil a large proportion of the trees which have escaped malformation by the insects. It is in connexion with the disposal of this material that the pine beetle investigation is primarily concerned in these areas, as it is particularly important that further damage to the crop should not take place as a result of pine beetle infestations.

The thinning experiment carried out at Swaffham during 1937 in a 16-year-old Scots pine plantation consisted in cutting out wolf trees with exceptionally large crowns with strong widespreading branches which threatened to crowd out and kill a number of surrounding trees. Most of them had developed multiple tops resulting from *Tortrix* damage at an early age. A number of very badly deformed trees including the worst forms of post horn resulting from *Tortrix* damage were also cut out, but every attention was paid to avoiding unnecessary reduction in the density of the stand. All dead and dying trees were cut and the remaining trees were " brashed "* to a height of about 6–7 feet.

Fortunately the pine areas are exceptionally easy of access for the removal of produce and are well situated as regards marketing facilities, and practically the whole of the poles can be either sold or utilised, so that only the badly shaped portions and the lop and top and the branches from the brashed trees remain to be dealt with, including very little material over 2 inches in diameter. Nevertheless, this mass of material presents rather a formidable appearance and certainly appears to be capable of forming a menace as suitable breeding material for pine beetles.

The thinning was carried out in strips 1 chain, 2½ chains and 5 chains in width and 5 chains in length, with unthinned areas 4 chains in width separating each of the thinned strips. Sample plots for the collection of fallen shoots were marked out in each of the thinned strips and in each of the intervening unthinned areas, also in the unthinned areas at each end of the experimental areas. The fallen shoots were collected at intervals throughout the autumn and winter as in the previous experiments. Owing to the presence of pine shoot *Tortrix*, a number of fallen shoots were found which were the result of the work of this insect. These shoots were counted separately. The results of the collections are given below :—

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* The term " brashed " refers to a method of pruning in which the lower branches are cut off close to the stem of the tree.

TABLE II.

Fallen Pine Shoots Collected in the Swaffham Experimental Area.

Position of sample plots	No. of fallen shoots destroyed by pine beetles	No. of fallen shoots destroyed by pine *Tortrix*
Unthinned area	Aveage 300 per acre	Average 130 per acre
Strip thinned 1 chain wide ...	,, 1,050 ,, ,,	,, 220 ,, ,,
Unthinned area	,, 490 ,, ,,	,, 275 ,, ,,
Strip thinned 2½ chain wide ...	,, 560 ,, ,,	,, 300 ,, ,,
Unthinned area	,, 365 ,, ,,	,, 230 ,, ,,
Strip thinned 5 chains wide ...	,, 1,540 ,, ,,	,, 240 ,, ,,
Unthinned area	,, 820 ,, ,,	,, 360 ,, ,,

Although the number of fallen shoots is rather higher in the thinned strip 5 chains in width, the results show that the infestation throughout the whole area is very low and indicates that this kind of material may with safety be left lying on the ground when thinning is carried out continuously throughout the compartment in this type of plantation.

The small number of shoots in the 2½ chain strip is probably accounted for by the parent beetle population being lower in the interior of the stand. This was found to be the case in trapping experiments in similar young pine plantations. On the other hand, the increase in number of shoots in the last unthinned area is probably due to the fact that this sample plot was near to a belt of old pines which stood along the edge of the plantation. The number of shoots destroyed by *Tortrix* is fairly equally distributed throughout the plantation, but is slightly higher in the sample plot nearest to the belt of old pine trees.

In order to study the development of pine beetle infestations in relation to the effects of leaving various types of material on the ground when carrying out the special form of treatment necessary in the pine areas in the eastern counties, another experiment was carried out at Broomhouse, near Brandon, in a plantation of Scots pine of the same age, and in other respects similar to the plantation at Swaffham, but the lay-out of the experiment was on different lines. Instead of carrying out the thinning in strips, there were four methods of treatment, each with unit plots one-fifth of an acre and three replications. The treated plots were distributed throughout the compartment and were separated by untreated areas.

The four methods of treatment were as follows :—

A. Plots to be brashed and thinned. Poles to be removed from the plantation and barked or burned. Lopped side branches also to be removed and burned. This is the control treatment so far as beetle attack is concerned, *i.e.*, all breeding material is removed.

B. Plots to be brashed and thinned. The lower rough-barked portions of the poles to be cut off and either barked or burned. The smooth-barked portion of the poles and the tops and brashed material to be left on the ground.

C. Plots to be brashed and thinned. Poles to be left lying in the length without trimming out. Brashed material to be left on the ground. This represents the cheapest method of dealing with unsaleable thinnings if there were no risk of beetle damage. It also provides maximum breeding facilities for any beetles present.

D Plots to be brashed. An advance treatment only to be given, *i.e.*, any injurious wolf trees to be felled. Butts to be cut off and left lying until the larvae of any beetles which have bred in them are fully developed. They should then be barked. These butts would thus function as trap billets. Brashed material and smooth-barked portion and tops of trees to be left on the ground.

The treatment of the plots was carried out in January and February 1937, and during the summer sample plots 1 chain by 1 chain were prepared in each plot for the collection of pine shoots. Three sample plots, X, Y and Z, of the same size were also prepared for the same purpose in the untreated part of the area.

As in the case of the Swaffham thinning experiment, the fallen pine shoots were collected during the autumn and winter of 1937–38, and the pine shoots which were destroyed by the pine shoot *Tortrix* were also collected and counted separately. The figures showing the results are tabulated below :—

TABLE III.

Fallen Shoots collected in the Broomhouse Experiment.

Sample plot	No. of pine shoots destroyed by pine beetles per acre		No. of pine shoots destroyed by pine *Tortrix* per acre	
A1	1,600	=1,220 average	260	=233 average
A2	1,390		320	
A3	670		120	
B1	4,320	=2,847 average	490	=343 average
B2	1,950		240	
B3	2,270		300	
C1	6,520	=3,933 average	490	=310 average
C2	2,420		200	
C3	2,860		240	
D1	2,450	=2,047 average	400	=327 average
D2	2,500		390	
D3	1,190		190	
X	1,850	=1,140 average	340	=270 average
Y	1,100		290	
Z	470		180	

The sample plots for each method of treatment show considerable variation, but the maximum figure for each method is not seriously high. The averages for A1, 2 and 3 and for X, Y and Z are very similar and represent the level of infestation in the untreated area. If we take these figures as a basis for comparison, the increase shown for the average infestation due to any particular method of treatment is not very high, but the figure for C1 indicates that the increase might become serious if this method were adopted continuously throughout the compartment. On the other hand, the modification represented by D indicates that the potential infestation can be reduced by half if D method is adopted, and could be still further reduced if a larger proportion of the stems were used as trap billets. The trap billet experiments also indicate that this material could be used to better advantage if placed along the edges of the rides than when left lying within the interior of the plantations.

The figures for the number of shoots destroyed by pine shoot *Tortrix* are of interest. They show that the distribution of the *Tortrix* throughout the compartment is fairly even, and the figures for Broomhouse and Swaffham are very similar. The average for Broomhouse is 296 shoots per acre and that for Swaffham is 251 shoots per acre.

The conditions existing throughout the crop in the Swaffham and Broomhouse experiments were very similar, in both cases there was very little variation, either in the density of the stand or in the average conditions of the trees in one part of the plantation as compared with another, so that similar treatment produced similar results, and the density of the infestation arising in any part of the crop can definitely be correlated with the method of treatment and the quantity of suitable breeding material available as a result of the treatment. This was largely due to the comparatively early age of the crop, the fairly regular growth and consequently the absence of large quantities of suitable breeding material in the stand before treatment and similarly in the portions which remained untreated.

Thinning Experiment in Delamere Forest.—The conditions existing in the experimental area in Delamere Forest were entirely different. As previously stated, this area was selected as being representative of the older-established Scots pine plantations, which exist in various parts of England growing at low elevation under conditions resulting in fairly rapid growth necessitating early and frequent thinning and which have previously been thinned, but were neglected during the early stages of development. Consequently it is not representative of crops which have received the attention necessitated by the combination of circumstances under which they have grown, examples of which are to be seen in a few well-managed pine areas in England. The plantation was 43 years of age, and although it has been thinned during recent years, the crop has obviously been badly neglected during the early stages of its development. In many places birch trees were allowed to crowd out the young pines and the crop became irregular. The largest pine trees irrespective of their shape were allowed to go ahead and kill out the slower-growing trees. As a result, the density of the crop has suffered and thinning is reduced to the periodic removal of dead and dying trees. The area was the only suitable plantation with the minimum length necessary for the lay-out of the experiment. In order to avoid very broken ground and rides, the lay-out had to be adapted to the conditions, and these determined the position of the widest thinned strip. This happened to be the most regular portion of the crop. The thinning was rather light and consisted in the cutting of dead and dying trees and a few of the roughest suppressed and subdominant trees. All the material above three inches in diameter was removed. This resulted in little more than lop and top and dead trees being left on the ground. This material was lightest in the thinned strip 5 chains in width and increased in quantity in the portion through which the 2½ and 1 chain strips ran. The sample plots were distributed throughout the area where the density of the stand was most regular, and the fallen shoots were collected throughout the autumn and winter of 1937–38. The results were as follows :—

TABLE IV.

Fallen Shoots collected in Delamere Forest Area.

Position of sample plots	No. of fallen shoots
Unthinned area	Average 2,860 per acre
Strip thinned 1 chain wide	,, 6,100 ,, ,,
Strip thinned 2½ chains wide	,, 4,463 ,, ,,
Strip thinned 5 chains wide	,, 1,447 ,, ,,

It will be seen that in this experiment the number of fallen shoots is least in the strip which represents continuous thinning throughout the compartment. Instead of reflecting the effects of the method of treatment, the results merely indicate in which part of the area the suitable breeding material was most abundant. The relatively high number of shoots in the strip thinned 1 chain in width is accounted for by the presence of several rather large pine tops. The results do, however, show that continuous thinning did not result in a heavy infestation.

Thinning Experiment in North-East Scotland.—Many of the older plantations in various parts of the north-east and north of Scotland are found at fairly high elevation under conditions resulting in slow growth which does not necessitate early thinning. Most of the areas of this description are in somewhat remote and more or less inaccessible localities as regards transport and market facilities, and the produce from early thinnings would in most cases be unsaleable. Thinning would, therefore, be an additional charge on the upkeep of the forest instead of yielding a profit or at least covering the cost of the operations. It will readily be seen that the necessity for thinning when the crop is say 20 years of age, and repeating the process every few years would entail expenditure which might ultimately render a probable financial return impossible in these cases, but high elevation, exposure and poor soil conditions form an ecological combination which result in retarded growth of the trees during the early stages, cause a more equal rate of growth, reduce the possibility of abnormal crown development in individual trees, and consequently produce a greater density of the stand during the early pole stage, because suppression and death of a large proportion of the trees by a comparatively small number of dominant trees does not take place as in the case of rapidly growing crops. The necessity for the regulation of the density of the crop by thinning does not therefore arise until a much later date, and by the time the necessity for thinning does arise, most of the trees which will be cut out in the first thinning are large enough to be of marketable size, and the whole of the rough-barked material, which is the most suitable material for the breeding purposes of pine beetles, can be removed from the area without additional expense. It will be seen that this results in the first thinning yielding a profitable return instead of a deficit ; it also provides for the disposal of all the material which is likely to provide facilities for an abnormal increase in the pine beetle population, and the necessity for subsequent thinning arises only at long intervals. These are points of great importance, which ought to be taken into account when considering the question of the cost of establishment and maintenance in relation to the financial returns from Scots pine plantations at high elevation in remote positions.

The high density of the stand in these slow-growing crops greatly increases their amenability to silvicultural treatment, as there is greater facility for the choice of trees to be selected for the final crop, and it is unfortunate that greater attention is not paid to the early selection of the stems likely to form the final crop, and to pruning these stems while they are of small diameter so as to enable them to produce clean timber free from knots. The conditions under which these crops are growing are those which produce pine timber of the best quality, and the low value of the land for any other purpose is an additional reason why the crops should be allowed to grow on long rotation, in which case they would produce a large volume of valuable timber per acre. It is a regrettable fact that thousands of acres of what are potentially among the finest Scots pine crops in Britain are at present entirely neglected from the silvicultural standpoint during the first 50 years of their growth. This is the period during which they should receive the greatest attention, as it is the only opportunity to ensure the production of clean timber.

Although in the aggregate large areas of this type of Scots pine crop exist in north-east Scotland, the particular requirements in regard to the lay-out of the large scale thinning experiment rendered the selection of a suitable area somewhat difficult, more particularly as regards equality in elevation and exposure throughout the area, and although the area ultimately selected was satisfactory in these respects, the elevation was lower and the exposure was less than occurs in many of the areas to which reference has been made. Consequently, the density of the stand was lower and the amount of suitable breeding material which had become available for the development of the bark-beetle population during the period previous to thinning was correspondingly greater, so that the resident bark-beetle population was probably at a higher level than would be the case in a stand growing under more exacting ecological conditions.

The area selected was a Scots pine plantation on the Glendye Estate, Kincardineshire. The crop was 48 years of age and had not previously been thinned. The experiment was laid out as in the previous cases, strips being thinned 1 chain, 2½ chains and 5 chains in width and 5 chains long ; unthinned areas 4 chains in width were left between each of the thinned strips, and sample plots were marked out in each of the thinned strips and unthinned areas for the collection of fallen shoots. The thinning was marked by the estate forester, Mr. Neil Macgregor, who also arranged for and supervised the cutting out and disposal of the produce and the subsequent collection of fallen shoots. All material in which the timber was over 3 inches in diameter was regarded as marketable and was removed before the pine beetles commenced to breed. This included all the rough-barked material. The average number of living poles cut out during the thinning was 225 per acre and these were fairly evenly distributed throughout the area thinned. The density of the stand after thinning was 550 stems per acre with an average quarter girth of 5¾ inches at breast height. The amount of breeding material left on the ground was 3,160 lineal feet of smooth-barked tops, with a maximum total diameter of 3½ inches including bark, and an average total diameter of 2½ inches, with a superficial area of 2,180 square feet of bark per acre. The appearance of the stand after thinning and the distribution of the breeding material is shown in Plate XVII, fig. 1. The fallen shoots were collected during the autumn and winter of 1937–38, and the results are given below :—

TABLE V.

Fallen Shoots collected in the Glendye Thinning Experiment.

Position of sample plots	No. of fallen shoots
Unthinned area	Average 942 per acre
Strip thinned 1 chain wide	,, 1,300 ,, ,,
Strip thinned 2½ chains wide	,, 2,477 ,, ,,
Strip thinned 5 chains wide	,, 3,706 ,, ,,

In this experiment the breeding material was fairly evenly distributed throughout the thinned areas ; the results may therefore be taken as representing the effects of the method of treatment and the increase in the number of fallen shoots can be correlated with the increase in the width of the thinned strips. The exceptionally low level of the infestation in the area representing continuous thinning is remarkable when it is remembered that the plantation was 48 years of age and had never been thinned. The number of fallen shoots (3,706), the average of 5 sample plots, each 1 chain by 1 chain, in the widest strip, which is the area of maximum density of infestation, represents only 1·7 shoots per square foot of bark or available breeding material ; an average of less than 7 shoots from each of the trees left standing, and less than one shoot per square yard of ground throughout the autumn and winter. An infestation of the density represented by this amount of destruction is of no economic importance and certainly does not warrant any expenditure on the destruction of breeding material. The infestation in the unthinned areas as represented by the number of fallen shoots is even more remarkable and shows quite clearly that the bark-beetle population in this type of unthinned plantation is extremely low. The parasite and predator population was at a very high level in the breeding material in the thinned strips and was largely responsible for the low level of the resulting pine beetle infestation, and the size of the resident population in the area previous to thinning indicates the degree of efficiency with which biological control had been maintained. The figures for the infestation in the unthinned area at Glendye are even lower than for the unthinned area in the Broomhouse experiment and not much higher than for the unthinned area in the Swaffham experiment, while they are much lower than for the unthinned area at Delamere. This indicates that the amount of suitable breeding material is greater in the unthinned area at Delamere than at Glendye, although the latter area has never been thinned, whereas the Delamere area unthinned in the present experiment had previously been thinned only a few years ago. This may be regarded as evidence that ecological conditions favourable for the rapid growth of Scots pine also provide more favourable conditions for the increase in the pine beetle population than exist in areas where the conditions result in slower growth due to such factors as increase in elevation, or exposure, but where conditions are otherwise favourable for healthy growth of the trees. This subject has been dealt with more fully by the present writer in a previous paper in discussing the effects of climatic and physical conditions on the development of the host tree, as factors influencing the density of the pine beetle population in Scots pine stands during the first 50 years of the development of the crop.

Results of Thinning during the Summer Months.—The above experiments have been entirely concerned with conditions which exist when thinning operations are effected during the winter months, the period during which this work is normally carried out. When dealing with the previous experimental work in the New Forest, it was stated that the experimental areas in Lodge Hill and Buskett's Enclosures were utilised during 1936 for other experiments, which for convenience would be described later. These experiments were for the purpose of ascertaining the effects of thinning during the summer months.

The thinnings were carried out in strips 1 chain in width, as in the previous experiments in these areas, but the actual thinning was done in July instead of February as in previous years, and all the poles cut out in the thinning were left on the ground. Sample plots for the collection of fallen shoots were laid out in strips thinned in July 1936, also in the strips thinned in February 1934, and in unthinned areas for comparison in each of the experimental areas. Fallen shoots were collected during the autumn and winter of 1936–37 in each of the sample plots and the results were as follows :—

TABLE VI.

Fallen Shoots collected during Autumn and Winter of 1936–37.

Experimental area	Average number of shoots per acre		
	Strip thinned July 1936	Strip thinned February, 1934	Unthinned area
Buskett's	1,850	770	800
Lodge Hill	1,080	880	720

Although a few *Myelophilus* did utilise the material during the summer of 1936 for the production of a late second brood, the resulting infestations were negligible. A matter of considerable importance was the fact that the material was very heavily attacked by *Pissodes notatus*, for breeding purposes. This might result in very serious consequences if there happened to be a young plantation of Corsican pine in the immediate vicinity, as *Pissodes notatus* has been found to cause serious damage in young Corsican pine plantations in various parts of England and Wales during recent years, by breeding in the stems of trees 3 ft. to 6 ft. in height, causing the death of the trees.

In order to find out to what extent the material would remain suitable for the breeding purposes of *Myelophilus* during the following year, the poles were left lying in the area throughout the next breeding season, and the fallen shoots were collected during the autumn and winter of 1937–38. The ground in the sample plots was first cleared so as not to include the shoots which fell as a result of regeneration feeding during the spring. This was necessary in order to compare the figures with the results of previous experiments. The results were as follows :—

TABLE VII.

Fallen Shoots collected during Autumn and Winter, 1937–38.

Experimental area	Average number of shoots per acre		
	Strip thinned July 1936	Strip thinned February 1934	Unthinned area
Buskett's	8,860	380	490
Lodge Hill	2,590	1,000	940

The figures indicate that there was a considerable increase in the infestation in the Buskett's experimental area in the strip thinned during July 1936, which shows that the material did remain to some extent suitable for breeding purposes, but was not very attractive. Considering that the whole of the poles were left lying on the area, including the rough-barked butts, the resulting infestation was very low.

In the case of the Lodge Hill experiment, there was only a slight infestation, but it must be remembered that the crop in Lodge Hill is 10 years younger than the crop in Buskett's, consequently the poles were smaller and included less thick-barked material.

The infestation in the other sample plots fluctuated somewhat, but the maximum infestation was at a very low level. The figures are of considerable interest, particularly those for the unthinned areas.

The experiment shows quite definitely that thinning during the summer results in less risk of *Myelophilus* outbreak than thinning during the winter. Perhaps the greatest advantage is that a much longer period is allowed for the removal of the produce without risk of an outbreak, as nearly a full year elapses before the principal brood completes its development in the year following the thinning. The risk of an outbreak of *Pissodes notatus* must not, however, be overlooked.

In addition to the experiments in Buskett's and Lodge Hill, a further experiment was carried out at Broomhouse in the eastern counties during 1936. This experiment was laid out in exactly the same way as the Broomhouse experiment in 1937, which has been described in the preceding pages, but the thinning was carried out in July, as in the case of Buskett's and Lodge Hill, and for the same purpose.

There was little sign of *Myelophilus* attack at Broomhouse during the summer of 1936, but the poles were so heavily infested by *Pissodes notatus* that it was considered too risky to allow the insects to complete their development, so the poles were peeled during the months of February and March 1937 and the larvae were collected.

A large number of the *Pissodes* larvae in the thin-barked portions had by that time been destroyed by birds, a point of importance which will be referred to later. In collecting the larvae, the contents of the thin bark and thick bark were kept separate, and in each case the superficial area of the bark was measured. Some of the larvae were destroyed during the process of peeling off the bark and a few dropped in the litter on the ground and were lost. The actual number of larvae was, therefore, rather higher than shown in the tables giving the numbers of larvae collected from the various sample plots. As the method of treatment for each set of sample plots was the same as in the Broomhouse experiment for 1937, described above, it will be seen that there was no material suitable for breeding purposes in Plots A, consequently there was no infestation in these plots. The figures for the other plots are as follows :—

TABLE VIII.

Plot	Area of bark per acre	Total	Average No. of larvae per acre	
			Pissodes	*Hylobius*
B	Thin bark=539 sq. ft.	539 sq. ft.	740	35
C	Thin bark=433 sq. ft. Thick bark=702 sq. ft.	1,135 sq. ft.	755 2,872 } =3,627	15 172 } =187
D	Thin bark=311 sq. ft. Thick bark=344 sq. ft.	655 sq. ft.	235 777 } =1,012	10 92 } =102

The above figures appear to indicate that the *Pissodes* larvae were more numerous in the thick bark than in the thin bark, but this was not actually the case. The lower number of larvae collected from the thin bark is accounted for by the fact that the activities of the birds were almost entirely confined to the thin bark, and it seems probable that few of the larvae in the thin bark would ultimately have escaped the attack of the birds and completed their development. The destruction of *Pissodes* larvae in thin bark occurred in the 1936 experiments in Buskett's and Lodge Hill in the New Forest and has been observed by the writer at various places in both England and Scotland, and seems to be a constant feature of the relationship between birds and *Pissodes.* In these circumstances it does not appear likely that the thin-barked material would form a menace if left lying on the ground even when the thinning is carried out during the summer in this type of plantation. On the other hand the thick-barked material would produce quite a considerable infestation, particularly as this generation would form a very strong nucleus which would probably give rise to a very heavy infestation in the material left lying in adjoining areas during the following year. In this connexion it must, however, be pointed out that the treatment in the case of Plots D stipulates that the thick-barked butts should be barked before the larvae complete their development. The butts would thus function as trap billets. In this case it will be seen that the operation would result in the destruction of 77 per cent. of the *Pissodes* larvae and 90 per cent. of the *Hylobius* larvae, and if the barking of rough-barked material is carried out in the case of Plots C the result will be the destruction of 79 per cent. of the *Pissodes* larvae and 92 per cent. of the *Hylobius* larvae. Incidentally this would also prevent any risk of a *Myelophilus* infestation arising from this material.

The results of the thinning experiments have clearly demonstrated that it is quite unnecessary to remove or destroy thin-barked unsaleable material under 3 inches in diameter and that this material may with safety be left lying in the forest, together with the lop and top, without risk of a severe bark-beetle infestation. It is in fact an advantage to leave this material in order that it may become incorporated with the forest humus and thus help to maintain the fertility of the soil and improve its mechanical properties. Observations indicate that the disintegration of the material can be accelerated if it is cut into small pieces, and there is no risk of insect development. The axil of the branch, or point of juncture with the stem, is one of the most favourable breeding places for many species of insects. Tops should therefore be trimmed out and should not be left lying intact.

The experiments have shown that it is an advantage to delay thinning operations until after the breeding season of *Myelophilus*. If the thinnings are carried out during July, August and September, there is no risk of *Myelophilus* attack, but the poles are liable to be attacked by *Pissodes* and *Hylobius*. However, this will not result in serious consequences if the poles are barked before the end of the following March. It will be seen, therefore, that thinning from July onward until October allows a much longer period for the removal of produce or for barking the material. It is important to see that all drains are kept clear of litter.

(2) *Trap Billet Experiments.*

In order to carry out a fairly comprehensive study of the use of trap billets in connection with the control or regulation of bark-beetle populations, a number of large scale experiments were laid out in pine areas in various parts of Great Britain. The distribution of the experiments was as follows :—

One in the New Forest.

Two in the Eastern Counties of England.

One in Delamere Forest.

Two in the north-east of Scotland.

Billets of the following types were used :—

Thick-barked, the bark of which was $\frac{3}{8}$ inch and over in thickness.

Medium-barked, the bark was about $\frac{1}{4}$ to $\frac{3}{8}$ inch in thickness.

Thin-barked, the bark was under $\frac{1}{4}$ inch in thickness.

Half of the billets had the whole of the bark left intact, the other half had a strip of bark removed along each side. This gave 6 types of billets, the length in each case being 3 feet.

The billets were arranged as follows : Two billets were placed flat on the ground, two billets of the same type were placed across and resting on the former. Each set of billets consisted of four billets of each of the six types.

Two sets of billets were placed along the sunny edge of the stand, four or more sets were distributed throughout the interior of the area. This arrangement gave 24 variations in breeding conditions, as there were 12 combinations of billet conditions arranged under each locality type.

The treatment of the billets, their arrangement in certain definite positions either directly on the ground, or off the ground, and their distribution either along the edge of the plantation or actually within the stand, was based on observations made on the various types of billets used in experiments in the New Forest and other places in the south of England during the previous years. For example, it had been observed that in certain cases when billets with strips of bark removed were used, the bark-beetle broods perished as a result of desiccation owing to the bark becoming shrivelled up before the larvae completed their development, while in other cases the broods perished before completing their development owing to the bark becoming detached as a result of the complete destruction of the cambium layer by the feeding of an excessive number of larvae. The object of the experiments was to obtain more extensive data in order to ascertain whether any particular result previously observed would manifest itself as a constant feature under any given set of conditions. In this respect it soon became obvious that billets with strips of bark removed could not be relied upon to give definite clear-cut results under any of the conditions existing in the experiments. They may therefore be ruled out as being unsuitable for general application for control purposes.

The thin-barked billets with the bark intact were definitely less attractive in all cases than the other types, and they also may be regarded as useless for practical purposes.

The medium-barked and thick-barked billets with the bark intact both gave excellent results, but in rather different ways. The thick-barked billets were definitely more attractive for *Myelophilus* and presented a larger surface for attack by this species when raised off the ground. The medium-barked billets were somewhat less attractive for *Myelophilus* but when lying in contact with the ground they were very attractive for *Hylastes* and *Hylobius* and were freely used by both these species for oviposition. As a certain amount of medium-barked material will always be available when rough-barked billets are being prepared, the most advantageous way to utilise this material will be to adopt a method which gives the best results for both types of material. This can be accomplished by placing two medium-barked billets flat on the ground and laying rough-barked billets upon and across them. The spot in which the billets are to be placed should first be cleared of coarse vegetation, and the medium-barked billets should be laid flat and nearly half buried in the soil.

The experiments also showed that billets placed around the edges of compartments give better results than billets placed within the area. This is particularly the case with plantations in the advanced thicket stage or the early pole stage, as for example in the areas in the eastern counties. This arrangement has the additional advantage that the billets are at all times visible from the rides and are not so likely to be overlooked or forgotten. Another point of importance is that the billets should not be placed where they are exposed to the full glare of the midday sun, although it is an advantage to have them in a warm, sheltered position. In the case of south aspects, they should be placed just within the stand so as to be afforded a certain amount of shade during the hottest part of the day. In other cases they will be better in the open, but close to the edge of the plantation, and should, if possible, be sheltered from the effects of cold east winds. The most suitable size is probably about 6 inches in diameter at the butt end, but size is of little importance and will be determined by the type of material available. In young plantations receiving early treatment, wolf trees will form the most suitable material and could with advantage be used for this purpose. For economical reasons the butt length should be cut to any length which will afterwards render the material serviceable for whatever purpose it is considered desirable.

(3) *Trap Stem Experiments.*

While carrying out observations in the New Forest and other pine areas in the south of England it was noticed that certain types of standing trees which had died from various causes, or had been broken off 12 to 15 feet from the ground, had acted as trap stems. These stems had been attacked by large numbers of bark-beetles ; in many cases the attack had been so intense that it had resulted in overcrowding the larvae and in some cases the entire population had been practically annihilated. These observations indicated that trap stems might usefully be employed to regulate bark-beetle populations if a type of stem could be found that could be relied upon to give constant results over a wide range of conditions. On the other hand, the fact that these stems were generally found to be heavily infested by predators, and often contained a large parasite population, led the writer to state in a previous paper that there is no certainty that the large scale use of trap stems and the removal and destruction of the bark will have the desired effect, as it might ultimately result in a chaotic series of interactions by combinations of factors cancelling out the effects of each other and end in futile effort and much useless expenditure.

With a view to finding out whether any particular type of trap stem had been devised which could be relied upon to give satisfactory results, the literature was examined. W. Sedlaczek (1921) described several types of trap stem, but his conclusions do not clearly indicate whether any of them could be relied upon to give the desired results. Some large-scale experiments were therefore planned in order to test certain types of stems which were considered to be most likely to give the best results. The trap stem experiments were laid out under various conditions in several parts of the country in the same localities as the trap billet experiments described above. The types of trap stem used were as follows :—

(1) Standing trees cut part way through on one side about 12 feet from the ground. The upper portion of the tree was allowed to fall over but remained attached to the standing stem. The bark was entirely removed for about a foot around the base of the stem.

(2) Standing trees with the top of the crown removed and the branches lopped off. The bark entirely removed for about a foot around the base of the stem.

(3) Felled trees with the whole of the branches left on.

(4) Felled trees with the whole of the branches cut off.

The whole of the stems were prepared in the autumn and winter of 1936–37. In each area the stems were arranged in sets, each set consisting of two stems of each type prescribed for the area. In England types 1, 3 and 4 were used. In Scotland types 2, 3 and 4. In each case one set of stems was prepared on the sunny edge of the stand, the other sets were distributed throughout the interior of the area, the number of sets being determined by the size of the area available. The size of the stems was determined by the size of the trees in the areas available for the experiments. In all cases badly shaped trees were selected. In the New Forest and Delamere Forest trees about a foot in diameter at breast height were used. In the eastern counties, at Swaffham, stems were only about 6 inches in diameter at breast height, and in Brandon Park one set of stems was composed of trees well over a foot in diameter and the remaining sets averaged about 10 inches in diameter. In both these areas type 2 stems were used instead of type 1, because of the difficulty in preparing the former satisfactorily, as the trees were very short. Type 1 gave very good results, but the difficulty of preparing the stem was very great as the upper portion would break away unless the tree was exactly the right length, so as to allow the top of the crown to reach the ground within a limited range, or if the top was too short to reach the ground, and equally good results were obtained by the use of type 4.

Type 2 gave extremely variable results in both England and Scotland. In some cases one stem would be infested to the point of overcrowding, while another stem of the same type standing within 50 yards of the former would be found to contain no bark-beetles, although sometimes heavily infested by *Pissodes*. This occurred more frequently in Scotland than in England. The uncertainty of the results renders type 2 quite unsuitable for practical purposes.

Type 3 was found to be unsatisfactory in many ways. On the whole the stems were fairly attractive, but the ones prepared on the sunny edge of the crop dried out too quickly and became unattractive at an early date, while those within the stand were not so attractive as type 4. The bark was very difficult to remove in most cases and the trees had to be trimmed out after they had become dry, which added to the cost. This type of stem was perhaps the most unsuitable of all.

Type 4 gave the best all-round results and were equally attractive in all the localities irrespective of the size of the stem. As in the case of billets, the stems were most attractive on the edge of the plantations in the young crops in the eastern counties. Although type 4 was considered to be the most suitable form of trap stem, it cannot be regarded as possessing any special merits which are not shared by billets. On the other hand it has certain disadvantages. Large stems require skilled labour for their preparation, they are more difficult to handle at every stage of the operations and a large proportion of the surface is only slightly attractive, as the bark-beetles tend to concentrate on the thicker-barked portion. In contrast, unskilled labour can be used for the preparation of billets, and only the portions of the poles actually used for the purpose require to be barked in order to destroy the bark-beetle broods, and this is more easily carried out than in the case of large stems. The evidence is, therefore, all in favour of the use of billets in preference to stems when special trapping of bark-beetles is necessary.

(4) *Pre-felling Treatment Experiments.*

Experiments were carried out in the New Forest, Delamere Forest, and in two areas in north-east Scotland to try to find a satisfactory way of treating standing trees so as to render the bark unsuitable for the breeding of bark-beetles when the trees are subsequently felled. For this purpose the sapwood was cut through with an axe at the base of the stem as in the normal preliminary step in felling operations. This was done in June and July after the main breeding season. The trees were left standing throughout the summer and autumn and were felled during the following winter. It was anticipated that the bark would be either unattractive in the spring after felling, or be too dry to permit the development of pine beetle broods. The results obtained varied considerably, in some cases the effects of the treatment were fairly satisfactory and the bark did dry out, causing the death of the bark-beetle broods, but in the majority of cases the effects were only slight and in some cases there was no apparent effect. This was particularly the case where the trees were growing in open situations and had short stems, large crowns, well developed root systems, and a large amount of sapwood which could not be completely severed. The experiments definitely showed that the method cannot be expected to give satisfactory results of practical value.

(5) *Discontinued Population Indicator Experiment.*

At one stage of the investigation it was considered desirable to correlate the number of fallen shoots with the actual number of bark-beetles responsible for their occurrence, so that it would be possible to calculate the amount of breeding material in the form of billets which would be required to trap the number of bark-beetles indicated by the presence of any given number of fallen shoots in any particular area. This would necessitate counting the number of exit-holes in the whole of the material from which the beetles had emerged. This would be a fairly simple matter, as the operation would be carried out in a newly thinned area and all the available breeding material within the area would be on the ground. Certain discrepancies of a limited character would be involved, as for example the degree of error made in distinguishing between bark-beetle exit-holes and those of parasites and the possibility that in some cases two beetles might emerge from the same exit-hole ; this, however, seldom occurs. The next step would be to find out how many pairs of beetles survived the winter and actually formed egg-galleries during the following spring and summer. For this purpose a fresh supply of breeding material would be prepared and all the egg-galleries which were formed during the next breeding season would be counted. This would theoretically give the ratio between the number of beetles which destroyed a given number of shoots and the number of beetles which survived the winter, and indicate the number to be trapped. From these figures the necessary superficial area of bark could be calculated. Up to this point the procedure appears quite simple, but further consideration shows that it would be necessary to carry out the operations in a large number of areas in which the density of the bark-beetle population differed considerably, so that it would be possible to ascertain whether the ratio between the number of bark-beetles and the number of shoots remained constant for different densities of infestation in different types of crops. It would also be necessary to ascertain whether the degree of mortality remained constant. It is clear that the construction of a density indicator table would present considerable difficulty, but the real difficulties are encountered when we consider its practical application in the forest on a large scale. The first step would be to ascertain the number of fallen shoots which occurred in any particular area. The collection of fallen shoots could not be made in permanent sample plots which would be kept clear of vegetation, as there is no guarantee that they would be representative of the whole area, as the intensity of infestation varies considerably according to the amount and distribution of suitable breeding material forming the source of infestation. This is shown quite clearly by the results of the experiments. In certain pine areas in various parts of the country the forest floor is fairly free from surface vegetation. In such areas it would be possible to select average sample plots by walking through the area and observing the average distribution. In the majority of pine areas in Scotland the rank growth of heather and other surface vegetation would render the selection of average sample plots by sight impossible, consequently the initial steps would be liable to result in considerable error. More important still is the fact that the number of pine shoots collected in one season cannot always be relied upon to indicate the number of beetles which will be present in the following year. For example, the number of shoots in the sample plots in a given area may indicate that there is no need to trap beetles, but if a few windfalls occur in the area during the winter, the beetle population in the following year may be very high as a result of these trees being used for breeding purposes. In order to assess the relative density of the population in such an area, two sample plots were laid out in an 80-year-old stand in north-east Scotland, where a few windfalls were scattered throughout the area, although no fallen trees occurred within the sample plots selected. The number of fallen shoots collected in one plot was 38,120 per acre and in the other 32,420 per acre, approximately ten times as many as the average number per acre in the thinned strips 5 chains in width in the Glendye experiment, where all the material under 3 inches in diameter was left lying on the ground, and 37 times as many as in the unthinned area in the same experiment. Numerous observations have been made during the subsequent progress of the investigation, and all the evidence indicates that the only certain way to keep the bark-beetle population at a low level is to prevent the insects having access to exceptionally favourable breeding facilities. In order to do so it is necessary to see that all suitable breeding material in the form of windfalls, snow-breaks, or felled timber, is either removed from the areas or barked before the bark-beetle broods have completed their development. These results show that the practical application of the method would probably lead to confusion and serious mistakes, so the idea was abandoned.

4. Results of the Bark-beetle Survey.

In addition to the large experimental areas, sets of stems were prepared on 91 estates for the purpose of collecting data as to the distribution of bark-beetles and their parasites and predators. Each set of stems consisted of six trees prepared as in the trap stem experiments, and in many cases two sets of stems were prepared ; 58 of these estates were in Scotland and 33 in England and Wales. Of the estates in Scotland 29 were Commission areas and 29 were private estates. In England and Wales 17 were Commission areas and 16 were private estates. Of the total 45 private estates on which sets of stems were prepared, in only one case was a charge made to cover the cost of felling. In the other 44 cases no charge was made for either material or labour. In every case the landowners, their factors, estate agents and foresters, showed great interest in the pine beetle investigation and did everything possible to facilitate the work. The Commission's staff were without exception willing to co-operate and help forward the work. These 91 estates, together with the areas where major experiments were being carried out, provided a total of 98 collecting centres, distributed throughout most of the important pine areas in Great Britain. In addition to the examination of the prepared stems, many windfalls, snowbreaks and trees killed by waterlogged soil, fire and fungi, were examined. Although Scots pine was the chief host tree dealt with, spruce and other species of coniferous trees were also examined in order to collect data about *Hylobius* and the various species of *Hylastes*. In this way much useful information was collected about the various species of bark-beetles and weevils and their natural enemies. Examination of the stems in the various localities verified the observations made in the trap stem experiments as to the relative merits of the various types of stems. Generally throughout the south and west of England the standing stems were fairly heavily infested, but in the eastern counties, the north of England and in Scotland, the infestation of the standing stems was very irregular. In some areas one stem would be heavily infested, while another stem perhaps 50 yards distant would be practically immune from attack. On the other hand, the felled stems, particularly those that were trimmed out, gave consistently good results in all localities. The examination of these stems showed that *Myelophilus piniperda* is abundant in most localities and that its numbers are, in most cases, entirely disproportionate to the extent of the pine areas, but depend more directly on the method of treatment of the pine stands. For example, in some localities in the north of Scotland where there are large blocks of pine there was little sign of serious bark-beetle damage, while on neighbouring estates it was obvious and extensive. On the whole, bark-beetle damage is of more frequent occurrence in pine areas in England than in Scotland. Examples of recent infestations and the way in which they were brought about will be mentioned later.

The standing stems were most disappointing so far as *Myelophilus minor* was concerned. It was anticipated that these stems would be particularly attractive to that species but in practice they were, on the whole, no more attractive than the felled stems, and in areas where *M. minor* was fairly abundant, the felled stems were equally heavily infested. For example, on an estate near Perth, *M. minor* was far more numerous than *M. piniperda*, and the galleries of the former extended right down to the butt of the poles. In some cases the galleries of *M. minor* were crowded together to a density of 70 per square foot of bark, but in spite of this density, owing to the wide spacing of the egg pockets and the manner in which the larvae feed in the bark, mortality due to overcrowding does not take place to anything like the same extent as in the case of *M. piniperda*. In nearly all parts of Deeside, *M. minor* galleries were found in the rough bark of standing trees down to within two or three feet of the ground, but the insect undoubtedly prefers the thinner bark and was particularly common in snow-breaks and windfalls in most parts of north-east Scotland at high elevation. The insect is certainly not so generally distributed as *M. piniperda* even in north-east Scotland and seems to be somewhat local in distribution. The stems prepared near Loch Morlick, at an elevation of over 1,000 feet on the northern edge of the Cairn Gorm Mountains, were heavily infested by *M. minor*, but other stems prepared near Loch Garten only a few miles distant showed no sign of *M. minor* attack. Its presence in remote localities, where remnants of the ancient Scots pine forests exist, suggest that the species is indigenous to Scotland.

Of the Hymenopterous parasites of *Myelophilus piniperda* the Pteromalid, *Rhopalicus tutela*, Walk. (=*R.* (*Pteromalus*) *suspensus*, Ratz.) was found to be by far the most numerous and widespread. This species was present in large numbers in every locality visited as far north as Sutherland and at all elevations where Scots pine grows and *Myelophilus* is present. *R. brevicornis*, Thoms., has a much more restricted distribution, and although it attacks *Myelophilus* it was more frequently found attacking *Pityogenes quadridens* in Scotland. Another species of *Rhopalicus* was found, but it has not yet been determined. Three species of *Roptrocerus* were found to be parasitic on *Myelophilus*, but they were not common on that host and appear to prefer other species. *Roptrocerus xylophagorum*, Ratz., was particularly numerous in the eastern counties and south of England as a parasite of *Polygraphus*. *Roptrocerus mirus*, Walk., was found in the eastern counties, at Tintern in the Wye Valley, in Delamere Forest, Cheshire, and as far north as Queen's Forest near Aviemore in the north of Scotland. *Roptrocerus eccoptogastri*, Ratz., was found only at Brandon in Suffolk, but the insect is probably present in many other localities. *Rhaphitulus ladenberghi*, Ratz., was also found only at Brandon. Continental records of the hosts of this species appear to refer only to Scolytids which breed in hardwoods. It seems probable, therefore, that this species will be found to be a common parasite of Scolytids attacking hardwoods in Britain.

In the Glendye district of north-east Scotland *Myelophilus minor* was very heavily parasitized by *Dinotus calcaratus*, Thoms. This species also attacks *M. piniperda* and *Ips acuminatus*, Gyll., but it appears to have a distinct preference for *M. minor*. Another species of the same genus, *Dinotus bidentulus*, Thoms., was found to be a parasite of *Scolytus ratzeburgi*, Jan., breeding in birch at Glenloy in north-west Scotland.

A species of *Eutelus* which has not been definitely determined, but is thought to be *Eutelus typographi*, Ruschka, was bred from *Myelophilus* material collected at Bogside near Stirling. *E. typographi* was evidently originally considered to be a primary parasite of *Ips typographus*, L., and the earlier continental records include the following hosts : *Ips typographus*, L., *I. chalcographus*, L., *I. quadridens*, Htg., *Myelophilus piniperda*, L., and *Polygraphus polygraphus*, L. But M. Seitner (1924) and F. Ruschka (1924) have shown that *Eutelus typographi* is really a hyperparasite. The former found it developing as an external parasite on the larva of *Ipocoelius seitneri*, Ruschka, which is a primary parasite of Scolytids and has been recorded from *Ips typographus*, L., *I. duplicatus*, Sahlb., and *I. amitinus*, Eichh. A single specimen of *Eutelus clavatus*, Ratz., was bred from *Pityogenes bidentatus* material collected in the south of England. This species is thought to be a hyperparasite of *Dendrosoter hartigii*, Ratz., as the *P. bidentatus* material was heavily parasitized by *D. hartigii* and no other parasites were present. *Eurytoma auricoma*, Mayr, was found to be generally distributed throughout Great Britain. A species of the family EULOPHIDAE, *Entedon methion*, Walk., was found to be a parasite of *Ernobius mollis*, L., in the south of England. The host is not a Scolytid and the record is mentioned merely as a matter of interest.

Of the BRACONIDAE, *Coeloides abdominalis*, Zett., and *Dendrosoter middendorfi*, Ratz., were found to be the most important parasites of *Myelophilus piniperda*, and the observations confirm the statement made in a previous paper, that these species prefer hosts which are breeding in standing trees, and are most abundant in dry localities. Both species have a wide range, and though more numerous in England, they were found in small numbers in the north of Scotland. *Dendrosoter protuberans*, Nees, was found only in the south of England in small numbers on *Myelophilus piniperda* and *Ips suturalis*, Gyll. *Dendrosoter hartigii*, Ratz., is common and has a wide range as a parasite of *Pityogenes bidentatus*, Hbst., and *P. quadridens*, Hart. It was also found as a parasite of *Pityogenes trepanatus*, Noerdl., and *Polygraphus polygraphus*, L., in Scots pine in Surrey. *Blacus trivialis*, Hal., was bred from pine beetle material from Delamere forest, Cheshire, and Tintern in the Wye Valley, but the exact status of this species is not known.

Individual specimens of other species of BRACONIDAE, ICHNEUMONIDAE and CALLICERATIDAE were bred from pine beetle material. Some of these parasites probably emerged from Lepidopterous hosts which had pupated in the crevices in the bark. Others are well known parasites of Diptera including SYRPHIDAE and TACHINIDAE, but a few species of these parasites are thought to have bred in the various Dipterous predators which were present in large numbers in the bark-beetle galleries.

The Dipterous predators mentioned in the previous paper were found to be fairly generally distributed throughout Great Britain and the following species were also found :—

XYLOPHAGIDAE ...	... *Xylophagus ater*, Meig.
DOLICHOPODIDAE ...	... *Medeterus apicalis*, Zett.
	Medeterus tristis, Zett.
LONCHAEIDAE ...	... *Lonchaea laticornis*, Meig.
	Palloptera usta, Meig.

Of the above species *Xylophagus ater* is the only one of importance. This species is numerous in the north of Scotland and appears to be present in most of the pine areas. The name *Xylophagus* is somewhat misleading as the larvae are extremely predatory. Although these larvae undoubtedly destroy large numbers of *Myelophilus* larvae their economic status, like that of the other Dipterous predators, is somewhat doubtful on account of the fact that they also destroy parasite larvae during the autumn and winter, when *Myelophilus* larvae are normally absent from the bark.

The other four species mentioned appear to be very local in distribution and not very numerous.

Two species of Neuroptera of the family RAPHIDIIDAE, *Raphidia notata*, F., and *R. maculicollis*, St., were found associated with *Myelophilus piniperda* and *M. minor*. The larvae of both these species destroy the bark-beetle larvae, but they are of comparatively little importance as bark-beetle enemies.

In addition to the Coleopterous predators previously mentioned, the following species were found in *Myelophilus* galleries :—

STAPHYLINIDAE ...	... *Quedionuchus laevigatus*, Gyll.
	Baptolinus alternans, Pk.
	Leptusa angusta, Aubé.

The above species were found only in Scotland and appear to be most numerous in the north and north-east.

Another species not previously mentioned is a member of the family COLYDIIDAE. *Aulonium ruficorne*, Ol. This species was found in the galleries of *Myelophilus* and other species in imported pit props in the ports of South Wales. The insect was previously recorded as a breeding species in this country in 1922, when T. Hudson Beare and H. St. J. R. Donisthorpe found it in the burrows of *Ips laricis* in Dean Forest.

In the previous paper it was stated that *Hypophloeus fraxini*, Kug., is a very rare insect in this country. The writer has since found it to be fairly numerous in certain localities in the south of England in the galleries of *Myelophilus* and other species.

The predatory Coleoptera are undoubtedly the most important natural enemies of bark-beetles. In an earlier paper the writer stated that he considered *Thanasimus formicarius* to be more harmful than useful, because of the destruction it causes to useful predator and parasite larvae. This opinion was based on observations in rather limited pine areas in the south of England under conditions where *Thanasimus* is of minor importance. Subsequent observations in the extensive pine forests of north and north-east Scotland have considerably modified that impression. Under natural forest conditions *Thanasimus* is extremely numerous and is a very formidable enemy of *Myelophilus*. Owing to the facility with which the *Thanasimus* larvae can burrow, they are particularly destructive to the larvae of *Myelophilus minor*. In some cases several full-grown *Thanasimus* larvae were found in a single *M. minor* gallery. Although *Thanasimus* is so numerous in the forests of north-east Scotland, the various species of *Rhizophagus* have no difficulty in holding their own, being everywhere very abundant. In fact, *Thanasimus* is not always the aggressor ; on one occasion the writer found several *Rhizophagus* adults actually devouring a *Thanasimus* larva. The latter had been attacked in the rear while half buried in a *Myelophilus minor* pupal chamber in the timber.

In several areas in north-east Scotland *Rhizophagus* adults were found to have been attacked by an entomophagous fungus, while they were clustered together in large numbers, hibernating during the winter under the bark of pine stumps. The fungus has been identified by Mr. T. Petch as *Hirsutella eleutheratorum*, Nees. A drawing of the fungus and the insect host by Mr. R. J. Spittle of Farnham House Laboratory is reproduced below.

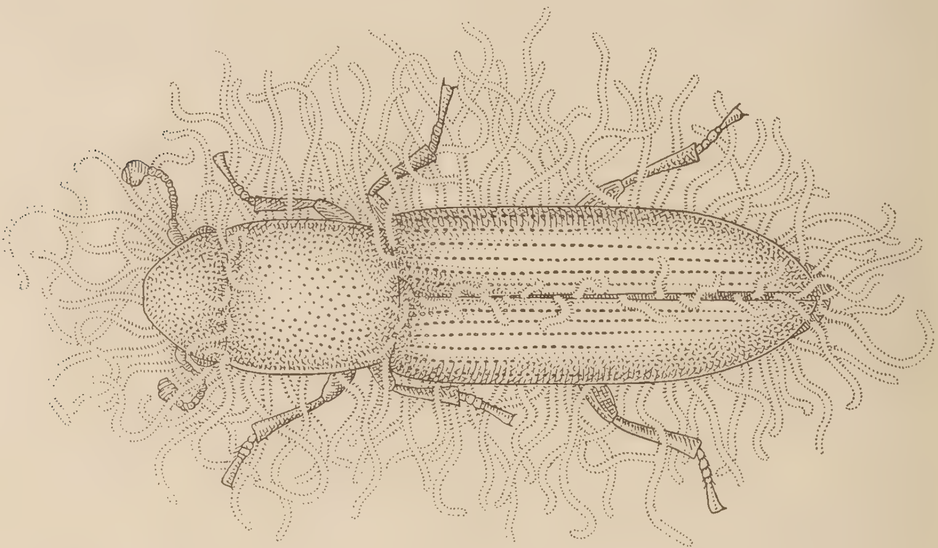

Fig. 1. *Rhizophagus* adult attacked by the fungus *Hirsutella eleutheratorum*, Nees.

Ips acuminatus appears to be most common in localities where *M. minor* occurs, and the conditions which favour the existence of the two species seem to be very similar. *I. acuminatus* has, however, a much wider distribution at present and extends over the whole of Scotland and the north of England. The position as regards the distribution of this species and *Ips laricis* appears to remain much the same as described by J. W. Munro (1919). The latter species is very common in the south of England and occurs in smaller numbers in the north of England and south of Scotland. It appears probable that both species are gradually extending their range, one spreading further north and the other spreading south along the eastern counties.

Similarly in the case of *Pityogenes bidentatus* and *P. quadridens*, the former is the common species in the south of England and the latter is the common species in the north of Scotland, but the two species overlap and both species and their varieties are to be found in many parts of Scotland. Little attention has hitherto been paid to some of these very small bark-beetles, and it is almost certain that several species are far more abundant than is generally supposed. Although *Pityogenes chalcographus* has been recorded occasionally it is probably often overlooked. It is normally a spruce insect, but the present writer has found it breeding in both spruce and Scots pine. In 1909 a single specimen of *Pityogenes trepanatus* was recorded by Dr. Joy as having been taken at Blair Atholl, and apparently this species was not seen again in Britain until 1938, when the present writer found it breeding in large numbers in Scots pine in Surrey. No doubt more careful search will reveal the presence of these two species in many parts of the country.

Polygraphus polygraphus, L., is another species which, although recorded near Scarborough some years ago, appears to have been entirely overlooked until quite recently. In 1936 Mr. Lewis, the forester on the Heveningham Estate in Suffolk, reported that the insect was killing large spruce trees on that estate. Similar damage was also reported from an estate at Melton Constable in Norfolk, and *Polygraphus* was found to be the insect responsible. The present writer visited both estates in 1937 and found that a considerable number of spruce trees of various sizes up to 70 feet in height had been killed. No pure stands of spruce occur in the areas. The spruce trees are scattered throughout rather open woods consisting chiefly of oak, with a few ash, birch and other species, and their presence is to provide roosting places for pheasants, consequently their destruction is of great importance from that standpoint.

Mr. Lewis stated that he noticed the unhealthy appearance of some of the spruce trees when he took charge of the woods four years previously. Some trees which he had kept under observation had gradually died from the top downwards and the process has taken three years. At first only 8 or 10 feet at the top of the trees showed signs of attack. In the second year about two-thirds of the foliage was dead, and the extension of the insect attack could be seen by the presence of resin exudation on the bark. In the third year the whole of the foliage died and the insect attack on the bark extended to within a few feet of the ground. No sign of insect or fungus damage to the roots could be found. Samples of bark were taken, and from this material the following species of Hymenopterous parasites were bred :—

Dendrosoter middendorfi, Ratz.
Roptrocerus xylophagorum, Ratz.
Rhopalicus tutela, Walk. (=*suspensus*, Ratz.)
Eupelmus urozonus, Dalm.

Of these parasites, *Roptrocerus xylophagorum* was by far the most numerous. This is a matter of particular interest in view of the fact that the writer, in a previous paper, in discussing this species, stated that although it had not been found to be very numerous as a parasite of pine beetles, it would probably be found to occur more frequently in Britain as a parasite of spruce bark-beetles, judging by the records of its hosts on the Continent of Europe. At that time the writer had not looked for it in anything but pine beetle material. The presence of this parasite in such large numbers should perhaps have been taken as an indication that *Polygraphus* was a species of long standing in Britain, but as *Pityophthorus pubescens*, Marsh., was found to be breeding in the lower branches of some of the spruce trees, it was thought that this species had probably formed a reservoir from which the parasites had spread to what was considered to be the more recently introduced *Polygraphus*.

The general impression received by the writer during the 1937 visit was that the combination of circumstances, namely the scattered distribution of the spruce trees throughout a rather open stand of light-crowned hardwoods, growing on a clay subsoil, caused the spruce trees to suffer severely from the effects of drought during the previous years, and that the effects of drought had been aggravated to some extent by the presence of numerous rabbit burrows surrounding the base of the trees ; and also by the destruction of the surface vegetation by the rabbits. It was considered that in the absence of *Polygraphus* the spruce trees would doubtless have made successful recovery. In these circumstances it was thought that the insect could not be regarded as being of primary importance where spruce is grown in pure stands with dense canopy. Moreover, as *Polygraphus* had seldom been recorded in Britain and was not considered to be of economic importance in Europe, it was thought that the sickly spruce had merely provided exceptionally suitable breeding facilities in which the insects had been able to become temporarily abundant. If these conclusions had been correct it would have been reasonable to expect the *Polygraphus* infestation to die out when the available breeding material became exhausted, particularly as the weather has been normal during the last few seasons, and the other spruce trees might reasonably be expected to remain healthy. However, the forester reported in March 1939 that the infestation continued to spread in 1938 and that trees had been killed which apparently were healthy during the previous year. This seems to throw an entirely new light on the economic status of *Polygraphus*, and the position has been rendered much more serious by the fact that in June 1938 the present writer found *Polygraphus* breeding in large numbers on the Albury Estate in Surrey. A very large Scots pine which had recently been felled was examined and both *Polygraphus polygraphus*, L., and *Pityogenes trepanatus*, Noerdl., were found to be breeding in thousands in the bark of the upper portion of the tree in company with *Pityogenes bidentatus*, Herbst. Mr. Bruce, the forester, stated that the pine tree had been dying from the top downwards for two or three years. The beetles were breeding in quite fresh bark during 1938, but an examination of the upper branches and stem showed that the insects had bred in those portions during the two previous years. Further enquiry elicited the information that large spruce trees had been dying on the estate for a number of years, and the description furnished corresponded with the conditions described on the estates in Norfolk and Suffolk. A large jagged spruce stump from which the stem had been broken in a gale seven years previously was examined and the bark was found to be perforated with tiny exit-holes, the size of those made by *Polygraphus*. A detailed examination of the bark revealed the presence of *Polygraphus* larval tunnels, and after much careful searching a dead *Polygraphus* adult was found in the bark. This discovery established the fact that *Polygraphus* has been present on the Albury Estate for at least seven years and it seems probable that the insect has been associated with the death of the spruce trees.

The fact that *Polygraphus* has not been regarded as a pest of primary importance by European entomologists proves nothing. Far too much reliance has been placed upon the opinions of Central European forest entomologists in the past, and too little attention has been paid to the collection of first-hand information in this country. This probably accounts to some extent for the present extremely unsatisfactory state of forest entomology in Britain.

Practically nothing is known about the distribution of the majority of the bark-beetles and little is known about the actual economic status of the root-feeding species. The survey has shown that *Hylastes ater* and *H. cunicularius* are abundant in many parts of Great Britain. *Hylastes opacus*, Er., is numerous in the south of England and extends throughout the north of England and south of Scotland. *Hylastes attenuatus*, Er., is extremely common everywhere throughout the south of England and the eastern counties and has spread as far north as Delamere Forest in the west. *Hylastes angustatus*, Herbst, is a very rare insect in Britain. This species and the two just mentioned, *H. attenuatus* and *H. opacus*, have been thoroughly confused both as regards museum specimens and the literature, but as the writer hopes to deal with these species later, no further reference will be made to them in this paper.

With the exception of *Myelophilus piniperda* and *M. minor*, *Hylastes ater* is probably the most destructive bark-beetle in Britain. The damage it does is, however, much less conspicuous than in the case of the two species just mentioned. *Hylastes ater* used to be regarded as of little importance, except in the case of very young trees, but the present writer has found it to be of importance both as regards hastening the death of mature pine trees and also in association with *Hylobius abietis* in the destruction of Scots pine in the early pole stage in the eastern counties. Two of these trees, 15 years of age, were growing in full light on the edge of a plantation bordering a ride ; in both cases they had made good growth during the current year, although at that date, 10th September, 1937, the foliage of the current year had wilted and turned pale green. In one case the growth during the last four years was as follows : 1937, 15 inches ; 1936, 21 inches ; 1935, 18 inches ; 1934, 25 inches.

In the other case the leading shoot during 1937 had been destroyed by *Tortrix* but the lateral shoots averaged 12 inches. The growth during the previous three years was as follows: 1936, 22 inches; 1935, leader lost and replaced by side shoot, 8 inches; 1934, 22 inches.

On digging out these trees and examining the roots there was no sign of fungus attack, but all the principal roots were found to be heavily infested with *Hylastes* and *Hylobius* larvae, and there were immature *Hylastes* adults feeding in the cambium, which showed that one brood had completed its development while the trees were still growing. Some of the *Hylastes* were still in the pupal stage. The *Hylobius* larvae were full-grown and were forming pupal chambers in the wood of the roots as shown in Plate XVII, fig. 3, so that the attack by both *Hylobius* and *Hylastes* took place while the trees were growing vigorously. Both trees had been attacked by *Myelophilus* during 1937 and one had 121 *Myelophilus* galleries and the other 120 galleries. In each case the superficial area of the bark attacked was 11 feet by 6½ inches. There were few exit-holes, and several parasite larvae were present in each case.

The whole of the cambium layer at the base of the stem below ground-level and around the thicker portion of the roots was a mass of *Hylastes* and *Hylobius* frass. Several *Hylastes ater* and a few *H. opacus* adults were feeding in those portions of the roots which had not been used for breeding purposes, and the bark on these portions of the roots was quite fresh. Plate XVII, fig. 2, shows some of these *Hylastes ater* adults feeding in this material. Another tree of the same age and size which had wilting foliage in September 1937 was dug up and examined on 24th January, 1938. By that date the foliage was quite dead. Every branch had been heavily infested by *Pityogenes bidentatus*, and the bark of the stem was closely crowded with *Myelophilus* galleries. The entire root system was found to have been heavily infested with *Hylastes*. There was no sign of fungus attack. A tree standing near showed slight signs of wilting foliage on the above date; on the bark of this tree there were numerous resin blobs showing where *Myelophilus* had attempted to enter the bark for breeding purposes during the previous season without success. There was considerable boring meal around the base of the stem, and on removing the bark 24 hibernating *Myelophilus* adults were found within a few inches of the ground. Many other trees along the edge of the compartment had boring meal around the base. The *Myelophilus* infestation had arisen from some poles which had been cut from a compartment on the opposite side of the ride during 1937. The *Hylastes* and *Hylobius* attack on the other trees resulted from a quantity of poles having been left on the ride during 1935 and 1936. Although these infestations were on a very small scale, they serve to show that *Hylastes* and *Hylobius* can, and do, kill trees which were in a healthy condition. These species are probably responsible for the death of far more trees than is generally supposed. In some cases they were found to be associated with the attack of *Pissodes notatus* on trees 4 feet to 6 feet in height. The writer has previously suggested that *Hylastes* and *Hylobius* probably predispose conifers to the attack of root fungi, it being thought that the beetle frass forms a suitable medium in which the fungus can develop and spread to the living tissues. In any case the trees so attacked by *Hylastes* and *Hylobius* would probably die, so that the attack of the fungi would be of little importance. *Hylobius* is probably the most destructive forest insect in Britain at the present time and is extremely numerous throughout the whole country, particularly in Scotland. *Pissodes notatus* is everywhere very abundant, even in the north of Scotland, but *P. pini* is the more numerous species in some parts of Scotland; this species also occurs in the north and eastern counties of England.

In connexion with the bark-beetle survey a visit was paid to the South Wales ports of Newport, Cardiff, Barry and Swansea, during July 1937. In each case imported pit props were examined both on the quay and in railway trucks loaded for despatch to the collieries. At each port thousands of bark-beetles were found to be emerging, although only a small percentage of the props were infested. The following species of bark-beetles were found in all stages :—

Myelophilus piniperda, L.
Hylurgus ligniperda, F.
Hylastes ater, Payk.
Hylurgops palliatus, Gyll.
Ips sexdentatus, Boern.
Ips laricis, F.
Ips erosus, Woll.
Ips suturalis, Gyll.
Pityogenes bidentatus, Hbst.

Although the wholesale importation of bark-beetles into South Wales may not have been a matter of great importance in the past, owing to the fact that the country was practically destitute of coniferous forests, the position will be entirely different when thousands of acres of coniferous plantations have been laid down during the next few years.

Peeled pine props recently imported from Finland were also examined. Many of these showed the mark of *Myelophilus minor* galleries on the surface of the wood, while larvae and pupae of *Pissodes pini* were found in pupal chambers in the wood. In every case these larvae and pupae were dead, evidently as a result of desiccation due to the removal of the bark. The above facts clearly demonstrate the danger of allowing the importation of pit props with the bark on.

Of the above species *Ips erosus* was the most numerous. This species has previously been recorded as breeding in Britain (Dean Forest), and the writer found it breeding in Scots pine stems at Bonvilston in South Wales in 1937. *Ips sexdentatus* has previously been recorded from time to time in the Forest of Dean and other localities. The writer found it breeding in Maritime pine at Pembrey in 1937. He also found *Ips suturalis* breeding in Scots pine at Bagshot in 1931. In the following year Mr. Donisthorpe found this species breeding in spruce in Windsor Park in considerable numbers. Individual specimens had previously been recorded in Scotland and the north of England under the name *Ips nigritus*, Gyll. Most species of bark-beetles that breed in coniferous trees seem to have a preference for certain species of host, but some species, like *Hylurgops palliatus* readily breed in either spruce or pine. This is probably the most widely distributed species in Britain, but it is of no economic importance as it does not attack living portions of the trees. It is, however, of considerable biological importance, as it helps to maintain parasite and predator populations at a high level of density, and thus acts as a reservoir from which these species can overflow and attack *Myelophilus* and other species when conditions become suitable for their increase. It has been shown that *Pityogenes chalcographus* and *Polygraphus polygraphus*, although regarded as spruce bark-beetles, will also breed in pine. *Dryocaetes autographus*, Ratz., is generally associated with spruce but the writer found it breeding in Scots pine in several localities. It has previously been regarded as a northern species, but the writer found it breeding in Verulam Woods in Hertfordshire and in the Forest of Dean. *Ips acuminatus*, Gyll., is generally associated with pine, but has been recorded from larch and Douglas fir ; in 1937 the writer found it breeding in spruce at Braemar. *Trypodendron lineatum*, Ol., appears to prefer spruce, but this species is particularly attracted to summer-felled Scots pine and is then of considerable importance because of its association with blue stain fungus under these conditions. It was found breeding in considerable numbers in summer-felled Scots pine near Ballater, and was extremely numerous in spruce in mid Wales. *Ips typographus*, L., is one of the most destructive beetles in spruce forests on the Continent of Europe. This species has from time to time been recorded in Britain but apparently has not yet become thoroughly established, probably because there are no extensive spruce forests in Britain. With the increase in spruce areas conditions will doubtless become more suitable and the insect will then become a pest unless steps are taken to keep its increase in check. All the bark-beetles that are commonly found in the south of England were present in a comparatively small area of mixed woods in the Isle of Wight.

Although not bark-beetles, three other species of beetles may be mentioned as they appear to be of some economic importance, and the damage they cause is of a technical character as they bore holes in the sapwood. One is *Molorchus minor*, L. This species generally prefers spruce but breeds in the larger branches of Scots pine in the eastern counties. This fact is of importance only as showing how insect populations can be maintained during periods when the normal host plant is absent. The larvae burrow in the surface of the wood and excavate pupal chambers in the timber. Another Longicorn beetle, *Tetropium gabrieli*, Weise, is generally supposed to breed only in larch. This is evidently not the case, as the present writer found *Tetropium* breeding in spruce in Kerry Forest in 1939. The third species is the Serricorn beetle, *Hylecoetus dermestoides*, L. This insect has been recorded as breeding in various hardwoods. The writer found it breeding in large numbers in spruce timber in mid-Wales and in larch at Dunkeld in Perthshire. This species appears to be very numerous in localities where it does occur and can be rather destructive.

It will be seen from the foregoing remarks that several species of bark-beetles have, during recent years, become established as breeding species in Britain, while several other species have considerably extended their range. The practice of referring to bark-beetles and other insects as being primary or secondary in importance is dangerous and misleading. Any species that is capable of doing damage may become of the utmost importance if the conditions become suitable for its increase. But none of the bark-beetles need become serious pests in Britain if proper precautions are taken to keep them under control. Nevertheless, it must be remembered that insects seize every opportunity to increase to the utmost extent of their reproductive capacity, and although under normal conditions their population density may be kept at a very low level as a result of destruction by their natural enemies, and the combined effects of various environmental factors which tend to restrict their rate of increase, they take advantage of every opportunity to increase in numbers. This increase may be brought about either by a reduction in the numbers of their natural enemies, or by the provision of exceptional breeding facilities. The writer has shown that practically the entire population of parasites and insectivorous predators can be eliminated from a block of forest simply by the removal of dead trees or other material in which the insects are present, while at the same time not a single pine beetle would be removed or destroyed. This can easily be avoided by removing all loose bark from such material and allowing the bark to remain in the forest. It has quite recently been stated that no bark-beetle outbreaks have occurred in Britain during recent years. Unfortunately this statement is far from accurate. It is quite true that no large scale outbreaks covering extensive areas of forest have occurred, such as from time to time are recorded in Europe, but that is largely because there are no extensive areas of pine forest in England and Wales, and few exist in Scotland. Nevertheless bark-beetle outbreaks have frequently occurred during recent years and the scale of magnitude has been determined to a great extent by the size of the pine areas concerned. The effects of these outbreaks may be seen in many parts of the country and can readily be detected by the presence of numerous spire-topped pines. These deformed pine trees can be seen in hundreds in practically all the older pine stands in England. Unfortunately the injury is not very apparent while the infestation is in its early stages, and the damage is often done before those in charge of the area realise that the outbreak is in progress. Failure to appreciate the significance of this destruction caused by the beetles at this stage, coupled with the impression that the subsequent destruction of the insects when they become abnormally numerous constitutes sound forest protection, is probably the cause of this neglect, and it cannot be too strongly emphasized that the insects should never be allowed to increase to the point where damage of this character takes place. Destruction of the insects after the damage has been done is merely an additional charge against the upkeep of a ruined crop. This method of dealing with insect populations probably has its origin in old text-book ideas of clean forestry. A good example of this type occurred during recent years in a well-known large pine area on the border of Surrey within a few miles of this Laboratory. In this case thinning operations were carried out extending over several years, during which period thousands of Scots pine poles were left lying in heaps during the breeding season. No attempt was made to control the beetles until the poles had been cut up and removed ; then a large number of men were employed in cleaning up the woods and not a twig was left lying on the ground. In the meantime hundreds of thousands of pine beetles had emerged from the thinnings and attacked the crowns of the standing pines in the recently thinned crop. In some cases not a single shoot escaped destruction on the uppermost three or four whorls of branches.

In another pine area in Cheshire an outbreak has been in progress several years. In this case a large area of pines which were growing on a low-lying piece of land near the centre of the forest were considered to be making unsatisfactory growth and it was decided to replace the pines with spruce. Owing to the frosty character of the particular locality, it was thought desirable that a number of the pines should be left standing in order to afford shelter to the new crop until the young trees got thoroughly established. Instead of cutting out the suppressed and unhealthy trees and leaving a shelter crop of the best pines, the latter were cut in order to produce immediate revenue and a large number of badly suppressed and unhealthy trees were left standing. These trees were immediately attacked by *Myelophilus* which were attracted to the felled area, and as the work of converting the crop has been in progress several years there has been a steadily increasing breeding ground for *Myelophilus*, *Hylastes* and *Hylobius*. Conditions have been so favourable for beetle increase that standing trees were attacked and reduced to a condition in which they were used for breeding purposes while the remaining foliage was still green.

Pine beetle outbreaks in Britain have not been restricted entirely to England. In the spring of 1938 the writer visited an estate in north-east Scotland on which there is a total of about 3,000 acres of pine forest. The estate factor informed the writer that he personally superintended the management of the woods as they could not afford to keep a forester. On visiting one of the blocks of pine forest, a gang of a dozen men were seen busily engaged in thinning a stand about 35 years of age which had not previously been thinned. The foreman stated that they were the employees of a timber merchant, that they were on piece work and that the thinning had been marked by one of the estate labourers. At least half of the dominant and subdominant trees were being cut out apparently quite regardless of any consideration as to leaving the best trees to form the final crop, or even the maintenance of an unbroken canopy. All the dead, dying, and undersized suppressed trees were left standing and only poles of the required dimensions were felled. In the autumn the writer paid another visit to this plantation and found the dead and dying trees were still standing. In the meantime the felled poles had been extracted and during the process large numbers of the standing trees had suffered very heavily by having large patches of bark torn away at the base. Plate XVIII shows the nature of this damage. Trees damaged in this manner are particularly liable to be attacked by *Hylastes*, *Hylobius* and wood-boring insects for breeding purposes. Even if the trees escape the attack of these insects, by the time occlusion of the wound takes place the sapwood is dead and may have become infested by fungus. Plate XIX shows the overthinned state of the crop and the large proportion of dead and dying trees which were left standing. On examination, some of the suppressed trees which still bore green foliage were found to have been infested by *Myelophilus piniperda* for breeding purposes. With proper treatment this crop would have developed into a first-class pine stand of considerable value, but it was completely ruined by a factor who professes to be keenly interested in British forestry. This case probably serves to illustrate how thousands of acres of what were potentially first grade pine crops in Scotland have been reduced to their present condition, and throws an interesting side-light on one reason why many British pine forests do not produce first grade timber.

Fortunately estates do exist in Scotland where the forests have been well managed, but in some cases the crops are either entirely neglected or are mutilated in the early stages of development, while thousands of acres of immature pine stands are being sacrificed at the age of 60 to 80 years instead of being allowed to develop into timber.

In each of the above cases the pine beetle outbreaks arose entirely through mismanagement and could easily have been avoided. In every instance standing pine crops were severely damaged and considerably reduced in value. In fact the crops would have been much better if they had been entirely neglected. Unfortunately in each case the person responsible for the maladministration claims to be an expert in silviculture. Other cases could be cited but the above will serve to illustrate the various ways in which pine beetle outbreaks arise, and emphasize the necessity for a wider and more comprehensive study of the principles underlying the development of insect populations in forests.

5. Bark-beetle Populations and their Development.

Density of a population refers to the number of individuals which exist within a given area or volume of material and is, therefore, relative to the area or volume concerned. The density may vary from point to point, but at any given point the density refers to that section of the population which occupies a definite fraction of the total area occupied by the entire population. It is, therefore, necessary in considering the density of a population, to define whether the whole or a part of the population is being dealt with ; and to ascertain whether the density of the population is regular or irregular throughout the area.

As we have seen, in the case of *Myelophilus*, the adult beetles feed in the shoots at the top of living trees, but the immature stage is passed in the bark of either standing trees, or logs lying on the ground ; so that the breeding material forming the food of the larvae is quite distinct from the food of the adult beetles. It is convenient to refer to the adult population in terms of density per acre or hectare of the crop constituting the host-plant. During the breeding season the adult beetles concentrate in the bark of trees or logs which are in a suitable state for breeding purposes ; the adult population can be estimated by counting either the number of pairs of beetles or by counting the egg-galleries, and the density of the population can be referred to either in terms of density per unit of breeding material, or density per unit of area of the crop. In the case of immature stages, we can ascertain the density per unit of each type of breeding material, and the quantity of each type of breeding material, and thus arrive at the density of the population.

The relative density of the population may, in the case of *Myelophilus*, be referred to in terms of damage done to the crop, because these insects, when feeding in the adult stage, cause pine shoots to fall ; and the number of shoots destroyed indicates the relative density of the pine beetle population and determines whether the insect population exists at a level of density of economic importance. This was the method which was adopted in carrying out the thinning experiments : the number of shoots being correlated on the one hand with the quantity and quality of the breeding material, and on the other hand with the age, area, and condition of the crop concerned. Although this method does not give the actual density of the insect population, but only the relative density in terms of the number of shoots destroyed by the population of beetles which emerged from a known quantity of breeding material of a definite quality, the results of the experiments show that the method was satisfactory in giving the solution to the problem as to what quantity and quality of material can with safety be left lying on the ground without risk of producing a bark-beetle population with a density of economic importance.

The experiments and observations also provide considerable evidence as to how the population densities of bark-beetles are governed ; how the density is caused to fluctuate and the manner in which fluctuations take place. Some writers on insect populations during recent years assert that there is for each species of insect a certain density at which balance or equilibrium takes place ; and that the population density tends to oscillate about this average density. This can only mean that departure from the average density takes place in opposite directions with a somewhat rhythmic sort of undulatory motion and that over a given period of time the departure from the average will be equal in each direction, that is to say, the rise and fall in the population density will be of equal magnitude leaving the average density unchanged. The experiments clearly show that this does not take place. On the other hand, they do show that in an unthinned forest, which is the nearest approach to conditions in a forest in the natural state, the combination of factors which result in mortality tends to limit the increase of the population, and that the insects are always trying to increase to the limit of their reproductive capacity. If conditions become favourable for an increase in the population, that increase will take place and the extent of the increase will be determined by the extent of the facilities provided. Successive increases in the population result in an increased average density. In the previous paper it was stated that in such areas predators and parasites are very numerous and, for a time, a state of biological control exists, its duration being largely influenced by the rate of growth of the crop. The trees tend to be more uniform in size in the case of moderately slow-growing crops than in very rapidly growing crops ; competition for light is less severe in the former, and fewer trees become suppressed and suitable for the breeding purposes of pine beetles at any given age than in the case of the latter. The rate of increase of the pine beetle population is determined by the amount of suitable breeding material that is available ; if the supply of suitable breeding material is limited, overcrowding takes place, resulting in great mortality among the brood. Overcrowding also facilitates the activities of predators, owing to the brood systems of the host becoming linked up, thus enabling the predator larvae to travel from one brood system to another. On the other hand, if the bark-beetle population is only on the borderline of overcrowding and the predator population is not strong enough to annihilate the brood, their activities may result in preventing overcrowding and thus enable beetle larvae, which would otherwise have been destroyed, to complete their development. This probably seldom occurs, but there is some evidence that it sometimes does. In the majority of cases the predators are extremely numerous, and unlike the specific parasites they are not entirely dependent on the bark-beetle larvae for food. The writer has reared *Rhizophagus* larvae to an advanced stage entirely on inner bark and has kept *Rhizophagus* adults alive for months by feeding them on this material. On the other hand, both *Rhizophagus* larvae and adults will readily devour almost any kind of animal matter. They have often been found feeding in numbers on *Hylobius* larvae which have been attacked by *Thanasimus* larvae, and on one occasion at Glendye the writer found eight *Rhizophagus ferrugineus* adults eating a small earthworm which had got under a piece of loose bark on a Scots pine pole. This omnivorous tendency doubtless explains how these insects maintain such a high population density. Parasites, on the other hand, are almost entirely dependent on the bark-beetles for hosts, although some species readily attack *Pissodes notatus* when the latter is breeding in thin-barked material. This question of the thickness of the bark is of great importance in limiting the activities of the parasites. *Rhopalicus* and other Chalcids are unable to reach *Myelophilus* larvae when the latter are feeding under thick bark, and the beetle larvae are then only liable to be parasitized when they burrow into the bark prior to pupation. In the case of thin and medium bark, parasites are often extremely efficient, and on many occasions the whole of the bark-beetle larvae in a brood have been found to be parasitized. This limiting factor has been referred to in the case of *Rhyssa* and *Sirex*, and the present writer has shown (1939) that under British forest conditions *Sirex* can only become numerous when large diameter material is available for breeding purposes. Similarly in the case of *Myelophilus*, thick-barked material favours increase. In both cases this enables us to manipulate the material so as to favour the parasites and facilitate their increase at the expense of the host insects. If the supply of suitable breeding material equals or exceeds the maximum requirements of the bark-beetles, the factor of overcrowding ceases to operate and biological control by means of parasites and predators also tends to break down. The maximum amount of suitable breeding material in the form of suppressed trees occurs when the crop reaches its maximum density. This is a little later than the correct time for making the thinning on silvicultural grounds, since the thinning should have been made before the crop actually reached that stage. The most rapidly growing portion of the crop determines the age at which thinnings must begin and the frequency with which they must be carried out. Similarly the most rapidly growing crops produce the greatest quantity of suitable breeding material for bark-beetles during a given period. In the case of slow-growing crops the first thinnings can be delayed for a much longer period and the state of biological control will normally be continued until the crop begins to open up, but snowbreaks and windfalls result in a rapid increase in the beetle population, if these occur on anything like a large scale. The snowbreaks and isolated windfalls are of great importance in the case of *Myelophilus minor* in north-east Scotland, and it is very important that this material should be dealt with regularly each year at the proper time in order to prevent the increase of the beetles. *M. minor* appears to prefer thin-barked material but will readily breed in thick-barked. The larvae of this species feed to some extent on the sapwood as well as on the inner bark, and when feeding in thin-barked material the larvae form their pupal chambers in the timber, but when feeding in thick-barked material they burrow into the bark to pupate. These habits and the fact that the egg-pockets are spaced wider apart have the effect of reducing mortality as a result of overcrowding and result in a large spontaneous increase in the beetle population when conditions are at all favourable. *Myelophilus piniperda* prefers thick bark for breeding purposes, and the examination of a large number of trees showed that the distribution is generally in the ratio of six egg-galleries in thick bark to one in thin bark.

Climatic conditions and geographic distribution play an important part in determining not only the potential rate of reproduction of bark-beetles, but also the actual rate of reproduction, *i.e.* what proportion of the progeny may attain maturity. In the south of England *Myelophilus* commences to breed early and some of the beetles after completing their first period of egg-laying emerge from the bark and after a period of regeneration feeding in the shoots, proceed to lay another batch of eggs about May. The thick-barked portion of the breeding material is often so congested by the first brood that the beetles forming a second brood lay their eggs in the thinner bark of the upper portion of the stems. These second broods are generally very heavily parasitized. At high elevation in the north of Scotland, *Myelophilus* is seldom able to produce a second brood ; and when this does happen, retarded development generally results in the second brood being decimated by the effects of severe climatic conditions. The potential rate of reproduction may also be reduced when the insects are, by force of circumstances, compelled to utilise unsuitable breeding material, or when excessive overcrowding takes place in material that is in every way suitable. The potential rate of reproduction may also be reduced by the action of nematode worms and other organisms. The rapid development of these organisms is greatly facilitated by excessive density of the bark-beetle population, and they undoubtedly exercise considerable controlling effect under these conditions.

The examination of a very large number of egg-galleries in the south of England showed that the average number of eggs laid was 120 per gallery, and this number has been taken as representing the potential rate of reproduction for the species in that area.

Although climatic and physical conditions do play an important part in limiting the population densities of insects, too much stress must not be laid on their importance. Some writers believe that physical factors are entirely responsible for limiting the activities of organisms. For example, there is a certain combination of temperature and humidity at which the individuals of a species will attain maximum duration of life, and at which the potential rate of reproduction will also reach its maximum. With every other combination the duration of life is shortened. The further removed from the vital optimum, the shorter will be the duration of life and a point exists where mortality occurs. From this it is argued that temperature and humidity are the decisive factors which determine not only the duration of life but even the possibilities of existence. It must, however, be conceded that if other conditions were not favourable, mortality would be just as inevitable even under optimum conditions of temperature and humidity, and since the vital optimum for any particular species would tend to produce excessive increase, overcrowding and consequent food shortage would automatically become the limiting factors in the absence of natural enemies.

On the other hand, the optimum conditions of temperature and humidity for any particular species approximate very closely to those for its natural enemies, consequently the latter tend to increase in a corresponding manner and must always form important factors in limiting the increase of the former.

A point of importance that appears to be frequently overlooked is the fact that the action of temperature and humidity as limiting factors is directly proportional to the extent of departure from the vital optimum and operates in inverse ratio with the approach to the vital optimum. The points of departure from the optimum at which mortality occurs are so remote from the optimum in most cases, that a considerable range of suitable conditions exist for the successful development of the population. In fact it is only within the range of these suitable conditions that the various species become of economic importance ; and the nearer conditions approach to the optimum the more likely is the insect to increase to pest proportions. Consequently the necessity for parasites and predators is greater as conditions approach the optimum for the host.

The present writer's remarks about the existence of a state of biological control in young pine stands are based on numerous observations and the examination of large numbers of dead and dying trees over a period of several years. Some figures recently collected by Mr. J. M. B. Brown, while carrying out some observations in the New Forest, provide confirmatory evidence. An analysis of these figures is given below :—

TABLE IX.

Data collected from two small Dead Pine Trees.

Type of bark	Length of section	*Myelophilus* :		Parasites :		
		Galleries	Exit holes	Exit holes	Larvae	Total
Thick ...	3 ft.	37	8	—	—	—
Thin ...	9 ft.	36	16	88	—	88
Thick ...	3 ft.	14	8	—	—	—
Thin ...	9 ft.	26	6	36	8	44
		113	38	124	8	132

In the two 3 feet butt lengths, 51 pairs of beetles with a total potential reproductive capacity of 6,120 produced only 16 young beetles. Mortality in these two cases was entirely due to overcrowding and destruction by predators. This mortality resulted in a decrease of 86 beetles in one generation, or in reducing the density of that section of the population to one-sixth of the density of the parent generation. In the two thin-barked portions, of the same trees, 62 pairs of beetles with a potential reproductive capacity of 7,440, produced only 22 young beetles. Mortality in these cases was partly due to desiccation and predators and partly to parasites. This destruction resulted in a decrease of 102 beetles or in reducing that section of the population to less than one-fifth of the density of the parent population. In these two thin-barked portions a total of 154 larvae actually survived the effects of predators and desiccation, and in the absence of destruction by parasites of 132 of these larvae, there would have been a net increase of 30 beetles. That is to say, the original population of 124 beetles would have increased to 154 beetles.

Taking the entire population of the two trees, 113 pairs of beetles with a potential reproductive capacity of 13,560, actually produced only 38 beetles. The beetle population was, therefore, reduced from 226 to 38 from one generation to another, the new generation being only one-sixth that of the parent generation. If a few large fresh felled logs had been available for breeding purposes the new population might have been anything from 38 to 13,560 in number according to the amount of destruction by parasites and predators. In the above example we may consider that overcrowding, desiccation and predators accounted for 98·75 per cent. mortality; while parasites accounted for only 0·97 per cent. mortality, and that the perpetuation of that particular population depended on a 0·28 per cent. survival. Nevertheless in the absence of parasites, instead of being reduced to one-sixth of its former density, the population would only have been reduced to about three-quarters. In the absence of predators it is certain that there would have been a substantial increase. The above 0·97 per cent. mortality due to parasites represented a parasitism of 77·65 per cent. of the beetle brood that escaped destruction by all the other factors.

Another small tree 23 ft. in height had been attacked by 85 pairs of beetles. Of these, 33 pairs had attacked the 3 ft. of the stem at the base of the tree, and although there was only about 2 sq. ft. of bark on this portion of the stem, overcrowding had not been so effective in destruction as might have been expected, and 165 beetles completed their development. In this section there was no parasitism. It seems probable that in this case predators had destroyed such a large proportion of the beetle eggs as to prevent overcrowding of the brood, and the net increase in this section of the population was 99 more than the parent population, an increase of 2½ times.

In the remainder of the stem 52 pairs of beetles had bred in the thinner bark. In this portion there was a survival of 101 young beetles, 3 fewer than the original number of parent beetles; 195 had been parasitized, giving a parasitism of 65·88 per cent. of the larvae, which had escaped destruction by other factors. In this case the total parent population of 85 pairs of beetles, with a potential reproductive capacity of 10,200, succeeded in producing 266 young beetles, slightly more than 1½ times the parent population, but it will be seen that in the absence of parasites the increase would have been 461, nearly 2¾ times the parent population.

In another case a small tree 26 ft. in length had been attacked by 55 pairs of beetles with a potential reproductive capacity of 6,600, but only 136 young beetles completed their development. In this case there was a net increase of 26 beetles, 308 of the brood having been parasitized. Mortality due to the combined action of overcrowding, predators, and desiccation had resulted in the destruction of 93·27 per cent.; parasitism accounted for 4·67 per cent., leaving a survival of 2·06 per cent. In the absence of parasites the survival would have been 444 beetles instead of 136. Here again, the apparently small percentage of parasitism actually represents a mortality of 69·37 per cent. of the larvae that survived destruction by the other factors.

In a few instances the *Myelophilus* appear to have entirely escaped attention by parasites, and in two such cases the trees were so lightly infested by *Myelophilus* that overcrowding could not have played any part in limiting the development of the broods. The two trees were attacked by 11 pairs of beetles and 267 young beetles completed their development. The potential population was 1,320, so the mortality may be considered to have been 79·77 per cent., and was probably caused almost entirely by predators. The *Myelophilus* population in these two trees had increased twelve times during the breeding season. This does not represent a net increase, because the population would still be subject to heavy mortality during the autumn and winter and again during the period immediately preceding the breeding season in the following spring.

In order to ascertain how the interaction of these various factors of control affect the average density of the bark-beetle population in pine stands, under normal conditions, the data collected from ten of these small dead trees have been tabulated, the results being as follows :—

TABLE X.

Myelophilus		Parasites		
Galleries	Exit-holes	Exit-holes	Larvae	Totals
36	44	50	—	50
73	24	88	—	88
55	136	285	23	308
7	154	—	—	—
4	113	1	—	1
71	512	179	22	201
35	86	150	17	167
85	266	195	—	195
40	14	36	8	44
29	95	85	20	105
435	1,444	1,069	90	1,159

The parent population of 870 beetles with a potential reproductive capacity of 52,200 actually produced only 1,444 young beetles, an increase at the end of the breeding season of only 1⅔ times the number of the parents. Mortality due to overcrowding, desiccation, and predators amounted to 95·01 per cent. Mortality due to parasites was 2·22 per cent., and the survival of progeny equalled 2·77 per cent.

Although the mortality caused by parasites appears trifling, it actually represents a parasitism of 44·53 per cent. of the population that escaped destruction by all other factors, and prevented the population increasing to three times the density of the parent population.

The above figures show quite clearly that the chances of survival of the bark-beetle brood under normal forest conditions in an unthinned pine stand are very few. Increase takes place in some places, and decrease takes place in other places, but on the whole there is only a slight increase in the density of the beetle population from year to year. The rate of this increase depends largely on the number and size of the trees that become available for breeding purposes. In slow-growing pine crops the trees are more regular in size and can be maintained at a greater density in a healthy condition at any given age ; in such crops fewer trees become suitable for breeding purposes and the density of the pine beetle population is maintained at a very low level.

It is not possible to indicate in figures the part played by predators in the control of bark-beetles, but the examination of immense quantities of breeding material in all parts of Great Britain, in almost every type of pine stand, and under a very wide range of combinations of conditions, has convinced the writer that predators are of the utmost importance as factors of control not only in the case of *Myelophilus* but also in relation to other species. They are of the greatest value in controlling the root-feeding species of the genus *Hylastes*, and they undoubtedly prevent these species from becoming the most formidable pest in coniferous forests.

As the pine crop gets older and the thickness of the bark increases, predators become of greater importance, and the percentage of parasitism decreases, as will be seen from the following analysis of data collected from a dead tree in a 60-year-old Scots pine stand in the New Forest.

TABLE XI.

Portion of stem	Nature of bark	Superficial sq. ft. area under bark	No. of *Myelophilus* galleries	No. of galleries per sq. ft.	Mean length of galleries in inches	No. of *Myelophilus* exit-holes	No. of parasite exit-holes	Percentage parasitism	No. of *Myelophilus* exit-holes per brood
20–25 ft.	Thin ...	4·4	3	0·7	2·3	1	1	—	0·33
15–20 ft.	Thin ...	4·8	22	4·6	5·8	20	70	77·8	0·91
10–15 ft.	Medium	5·4	42	7·7	5·0	180	72	71·4	4·29
5–10 ft.	Thick ...	5·8	82	14·1	4·46	256	24	8·6	3·12
Below 5 ft.	Thick & rough	6·9	142	20·6	4·0	244	13	5·1	1·72
			291		4·37*	701	180	20·4	2·4*

* Average.

It will be seen from the above figures that *Myelophilus piniperda* definitely prefers the thicker bark for breeding purposes, and that the infestation decreases in density with reduction in thickness of the bark. The average length of the galleries increases as the density of the infestation decreases, until the very thin bark is reached. Then conditions become unsuitable for *M. piniperda* and the galleries are very short. Mortality in this portion was probably due to desiccation ; this is very often the case. In the remainder of the tree the percentage of parasitism increases with the decrease in thickness of the bark. A total infestation of 291 pairs of beetles, with a potential reproductive capacity of 34,920, produced only 701 young beetles, an increase of only 119, and a total of $1\frac{1}{5}$ times the number of the parent population. In this example overcrowding, desiccation and predators, accounted for 97·47 per cent. mortality ; parasites accounted for only 0·52 per cent. mortality, and only 2·01 per cent. of the potential population survived to carry the infestation over to the next breeding season. It will be observed that in this example parasitism only amounted to 20·4 per cent. of the brood that escaped destruction by all the other factors.

Nevertheless, this percentage of parasitism is of the utmost importance and might quite easily make all the difference between an increase or decrease in the insect population. As previously mentioned, the beetles which completed their development and emerged from the bark are still liable to destruction before the next breeding season, and an additional percentage of mortality equal to that caused by parasitism would in this case result in a decrease in the population. J. J. Karpinski (1935) has shown that in Poland, under normal forest conditions, the combined action of all environmental factors which limit the increase of *Ips typographus* resulted on the average in a total mortality of 97·4 per cent. of the brood, so that on the average only 2·6 per cent. emerged as adults. As there will be a certain amount of mortality in the adult stage there is little chance of the population increasing in density from year to year.

The foregoing examples illustrate the fallacy and futility of theoretical population studies based entirely on mathematical calculations of the so-called interactions of hosts and parasites, which are supposed to enable entomologists to predict the probable course of development of insect populations.

The combination of factors involved in the regulation of insect populations differ for each type of insect and with each type of environment. Each problem can be solved only by intensive study of the actual conditions concerned ; by the unprejudiced evaluation of all the factors involved whether biotic or abiotic, and the correlation of extensive field observations with the results of carefully planned experiments.

Although the particular species of insect constituting the pest must in all cases occupy the centre of the field, its importance is relative to the nature and extent of the damage which it causes, and it can only be studied in the true perspective in relation to the host plant concerned, since the latter constitutes the reason for the investigation. Consequently, an ecological study of the host plant must necessarily be of fundamental importance, together with a study of cultural methods and the effects of these cultural methods on the host plant, the host insect, and the parasites and predators associated with the latter. It will be seen, therefore, that the problem of host relationship cannot be solved by theoretical studies of imaginary parasites in relation to imaginary host insects with theoretically stable environmental conditions. These problems can be solved only by practical studies which embrace, in each individual case, the whole problem of the relationship of the insects to the host plant and to other host plants and insects forming part of the biological association, and the abnormal climatic and physical conditions which play such an important part in causing fluctuations in the density of the insect populations.

The really important point in these investigations is to find out the vulnerable spots in the life-cycle of the host insect and then to concentrate on ascertaining how this knowledge can be utilised so as to facilitate the work of the parasites and predators. This was the method adopted in the case of wood-wasps and bark-beetles and in each case it has been shown that with a little assistance on the part of the forester both these types of pest can be controlled by their natural enemies. Incidentally it is of interest to note that both these cases have, during recent years, been cited as examples of forest pests which were not amenable to treatment on biological control lines. It has, however, been shown that these insects can be controlled by their natural enemies under normal forest conditions and the population can be maintained at or below the level of economic control when proper attention is paid to forest hygiene under silvicultural conditions. Neglect to attend to windfalls, snowbreaks, thinnings, fellings, and unsanitary conditions caused by fire or water-logging of the soil, results in a rapid increase in the population density and may cause an outbreak.

Although the extent and magnitude of a pine beetle outbreak largely depends on the quantity of material available for breeding purposes, it also depends to a great extent on the density of the bark-beetle population that exists within the area when the exceptional breeding facilities occur, consequently it is of the utmost importance that the resident bark-beetle population should be kept as low as possible.

K. E. Schedl (1937) has shown that the average density of the bark-beetle population increases with the advance in age class of the crop in the case of the spruce bark-beetles, *Ips typographus* and *I. chalcographus*. In 38 blocks of well managed forest with a total of 7,960 hectares, he examined 21,007 trees and found that they were infested as follows :—

TABLE XII.

Age of crop (years)	No. of stems examined	Percentage of stems infested by *Ips typographus*	Percentage of stems infested by *Ips chalcographus*
21–40	6,781	1·8	10·7
41–60	5,796	5·1	15·4
61–80	4,649	7·5	25·7
81–100	3,209	14·9	41·7
Over 100	572	12·7	57·8

In order to assess the density of the infestations he examined three samples of bark 10 × 100 cm. on each stem, one at a metre from the ground, one in the crown, and one in the middle of the stem. The average density of attack was as follows :—

TABLE XIII.

Age of crop (years)	Density of infestation by *Ips typographus*	Density of infestation by *Ips chalcographus*
21–40	5·5	18·8
41–60	6·4	18·2
61–80	7·1	18·3
81–100	10·9	26·9
Over 100	9·0	34·7

He points out that the average density of the bark-beetle population in a natural forest depends on the amount of breeding material which becomes available as a result of competition among the trees, whereas in a cultivated forest it depends on the amount of material which becomes available as a result of exploitation operations, and the danger of an outbreak is not less under silvicultural conditions than under natural conditions. In fact, he considers that the danger may be greater under silvicultural conditions owing to an increase in the average density which may occur as a result of the accumulation of breeding material in the form of unsaleable material during thinning operations, frequency of fellings and delay in clearing debris. In a healthy forest where there are only a few trees suitable for breeding purposes the percentage of the infestation with reference to the total number of trees is very small, but with regard to the available breeding material it is very high. The density of the infestation is likewise high and the progeny per surface area of bark is correspondingly constant and tends to equal the number of parent beetles. The above statements confirm the observations of the present writer as regards conditions in Scots pine forests and the population densities of *Myelophilus*.

Schedl points out that with the exceptional increase in the amount of available breeding material, all these relations change considerably. The large increase in suitable breeding material results in the wider distribution of the beetle population, the percentage of infestation increases and the density per unit of breeding material decreases. As a result the combination of factors of resistance which kept the population at a low level in a healthy forest decrease in effectiveness or may cease to operate. This especially refers to mortality due to overcrowding as a result of limitation of suitable breeding material. As the resistance of the environment decreases, the co-efficient of reproduction, or number of progeny per parent increases. When the breeding material becomes unsuitable and breeding facilities are again restricted the population density again declines. Schedl notes that when an outbreak occurs owing to exceptional increase in breeding material, as for example, when an extensive windfall occurs, the intensity of the infestation depends on the amount of suitable breeding material and on the average density of the beetle population existing before the favourable conditions arose. In the first season of the outbreak, the increase of the population is comparatively limited but in the second season the available breeding material is fully exploited and there is a great increase in the beetle population. This increase may be maintained if the necessary increase in breeding material takes place, but if no further increase in suitable breeding material occurs, a mass attack on the standing trees takes place and many apparently healthy trees may succumb.

After a severe storm a general survey should at once be carried out and a plan of campaign arranged so as to facilitate the clearing of the area at the earliest possible date. It is not, however, sufficient simply to remove the fallen trees or to destroy the broods which exist in the material ; it is necessary to concentrate the attack on a limited number of stems which are easily accessible for inspection and treatment. In other words, in all circumstances one must try to prevent the insects which are attracted to the area from attacking the standing trees and breeding in the weaker ones. If this is allowed to occur control measures are useless. In the case of spruce this is achieved by preparing a sufficient number of the blown stems by cutting them off at the base and thus rendering them more attractive. The success depends on the time at which the storm occurred, and the number of men available. Schedl states that the following numbers of unbarked trees should be left :—

TABLE XIV.

Age of stand (years)	Percentage of stems to be prepared	Minimum number per 1,000 stems in the stand
21–40	2	1
41–60	5	2½
61–80	8	4
81–100	15	7½
Over 100	12	6

If, for example, the stand is 30 years of age, and there are 300 trees per hectare blown, 6 are left as trap trees, but if 100 stems per hectare have been blown and the stand consists of 5,800 stems per hectare, then the number of trap stems must not be less than 6. The trap stems should be numbered and should be inspected and the bark removed before the bark-beetle larvae are half-grown. The lop and top should be piled into heaps and should be burned after oviposition has been completed. These stems, he states, should be prepared whether or not the area can be immediately cleared.

During and after an outbreak it is necessary to pay special attention to the inspection of standing crops in the vicinity in order to ascertain what proportion of the standing trees have been attacked by the beetles. Stems within the stand which have been attacked should be felled and barked in order to destroy the broods, and in the following spring two stems should be prepared to replace each stem which has been felled and barked, provided that no other windfalls have occurred in the meantime. The stems selected for traps should be such as would normally be removed during a thinning. Even in stands where no infestation is observed stems should be prepared as a precautionary measure during the spring immediately following the outbreak. Schedl states that the number should be two stems per hectare irrespective of the age of the stand. Even in the event of the whole of the timber being utilised, it will be necessary to leave 10 per cent. of the stems unbarked. These stems should be barked before the broods are half-grown.

During recent years much attention has been paid to the problem of the control of bark-beetle infestations and outbreaks in Europe and various forest entomologists have from time to time produced mathematical formulae for the purpose of estimating the extent of the outbreaks and calculating the amount of material which they consider will be necessary to trap the beetle population, which they estimate will occur in the season following the year in which exceptional facilities for abnormal increase has occurred. The various authorities disagree as to the efficacy of each other's formulae, so these methods will not be described. M. Seitner (1924) studied an outbreak of *Ips typographus* which occurred in the Austrian Alps in 1921–1922, and elaborated measures for the control of this species. Z. S. Golovyanko (1926) described methods for estimating pine beetle populations and the control of outbreaks. He considers that in forest stands with a large number of beetle-infested trees, the laying out of trap stems taken from the healthy trees leads to an increase of the reproductive capacity of the bark-beetles on standing trees, since the total area of available breeding material is increased. It can therefore be looked upon as a completely useless measure in spite of the entirely apparent effectiveness manifested in the reduction of the bark-beetle progeny of the beetles which infest such stems. He points out that almost the same results can be obtained by felling and barking a corresponding number of infested trees before the broods complete their development. He also draws attention to the fact that in healthy forests the density of the bark-beetle population is largely governed by overcrowding in the limited quantity of available breeding material in the form of suppressed and over-mature trees and that trapping in these circumstances merely increases the amount of suitable breeding material and tends to relieve congestion in the normal breeding material. A. Il'inskii (1928) continuing the work of Golovyanko confirms the views expressed by the latter and says that the chief emphasis in the control of bark-beetles should be laid on the limitation of the supply of suitable breeding material during the normal forestry operations. In the case of a focus of infestation existing owing to abnormal conditions in any particular locality, it is advisable to eliminate the pest by the timely felling and barking of infested trees.

I. Trägårdh & V. Butovitsch (1935, 1938) described the effects of severe storms that devastated the pine and spruce forests of central and southern Sweden in 1931–1932, resulting in severe bark-beetle outbreaks. The damage done by the bark-beetles was minimised in those cases where it was possible to remove or bark the fallen timber before the broods developed. An experiment was carried out in which strips of bark were removed from all pieces of timber over 4 inches in diameter in order to increase the resinous smell and render the logs more attractive, and also to destroy the subsequent broods as a result of the bark drying out. This was very satisfactory with spruce and resulted in the destruction of 95 per cent. of the broods of *Ips typographus*, L. With pine, however, this method produced only a 34 per cent. destruction of the broods and was not considered worth while, as complete removal of the bark ensures almost complete destruction.

Experiments were made in stacking timber in the forest and covering the stacks of timber with moss and faggot wood to prevent bark-beetles attacking the bark. This method protected the stacks of timber from the attacks of beetles that prefer light, such as *Ips typographus*, *Pityogenes chalcographus*, *Myelophilus minor*, *Ips proximus* and *Monochamus sutor*, but was useless against those species which normally infest roots, such as species of *Hylastes* and *Hylobius*. A covering of 19 inches thick was not always proof against *M. piniperda*. Pine is very susceptible to the attack of fungus causing blue stain of the sapwood, and is not suitable for stacking in the forest. Although bark-infesting species perished in stacked timber from which strips of bark had been removed, *Xyloterus* (*Trypodendron*) *lineatus* appeared to prefer this material and developed in it normally.

During the investigations carried out in the windfall areas in Sweden, the authors calculated that normally 47 per cent. of the bark was suitable for the breeding purposes of *Myelophilus piniperda*, but owing to the roots of the blown trees remaining attached to the soil on one side, only 49 per cent. of the blown pines were suitable for breeding purposes, so that in the first year only 23 per cent. of the material was available for the breeding purposes of *M. piniperda*.

In the case of spruce 82 per cent. of the bark was normally suitable for the breeding purposes of *Ips typographus*, but owing to the roots of the blown trees being attached to the soil on the leeward side of the trees, only 7 per cent. of the spruce bark was actually available for breeding purposes during the first year.

When, however, the trees are cut off from the stumps, the resistance is eliminated and the spruce bark area available for *Ips typographus* is then 82 per cent. of the total; and for *M. piniperda* the available area of pine bark is 43 per cent. of the total. The above figures indicated that during the first year of the outbreak the increase of *Myelophilus* would be much greater than that of *Ips typographus*, but in the second year of the outbreak *I. typographus* would increase to a much greater extent than *Myelophilus*. Because of this, and also because of the fact that pine timber is much more liable to reduction in value due to blue stain fungus when the bark has been used by bark-beetles for breeding purposes, attention was concentrated on clearing and utilising the pine timber.

It was found that the average density of the population of *Ips typographus* increased from 20,000 per hectare in 1931 to 158,000 per hectare in 1932; and rose to an average of 2,367,000 per hectare in 1933.

The main object of the survey was the collection of data which could be used as a basis for calculating the amount of breeding material which would be necessary in order to trap the bark-beetles that developed as a result of the exceptional breeding facilities provided by the abnormally heavy windfall. Although a very accurate, detailed survey was made, the results seem to indicate that the figures obtained are of little value for the purpose of calculating the probable extent of the infestation in the following year, or the amount of material that should be prepared for trapping purposes. Figures are given for seven areas showing the density of the population in 1932, and the rate of increase in 1933. They are as below (Table XV).

The densities of the infestations in 1933 bear little resemblance in order of magnitude to those of 1932. For example, the lowest infestation of 1932 was 111,000 per hectare and gave rise to the heaviest infestation of 3,544,000 per hectare in 1933. The next heaviest density in 1933 occurs in an area which showed no infestation in 1932. In this area in 1931 only single trees were blown. These trees were scattered throughout the area and lay in the shade of the standing crop, consequently they remained unattractive until the following year, when an invasion occurred from other areas giving rise to a population of nearly 3,000,000 beetles per hectare in 1933, while the two infestations with the highest densities in 1932 both give rise to infestations which are well below the average in 1933. In these circumstances it is difficult to see how the figures for the 1932 infestations can be satisfactorily used as a basis of calculation for predicting the quantity of material that would be necessary to trap the beetles in the following year.

TABLE XV.

Size in hectares	Density per hectare	
	1932	1933
4·5	—	2,921,000
4·0	111,000	3,544,000
2·0	159,000	1,645,000
1·0	159,000	1,965,000
0·8	175,000	2,297,000
0·7	242,000	2,092,000
1·5	259,000	2,106,000

Even in cases where the density of the infestation can be accurately assessed, there is no means of ascertaining what percentage of the population will be destroyed by predators during the following spring before the beetles succeed in establishing themselves in the breeding material. Under normal conditions in Britain, birds are of very little importance as factors of control. But in the case of an outbreak the authors have shown that in Sweden, birds and predacious beetles, particularly Clerids, destroy enormous numbers of bark-beetles during the swarming period in the spring. This mortality they estimate may range from 50 to 95 per cent. of the adult beetle population. The impracticability of estimating the probable amount of this mortality renders the method very unreliable, especially as the density of the infestation may vary tremendously in different parts of the country or even in crops of different age classes within the same area, because, as has already been pointed out, the density of an infestation in any locality largely depends on the original density of the resident population before the windfalls occur, as well as on the quantity of extra breeding material that becomes available. But as the above figures clearly indicate, if the outbreak is allowed to develop, the possibility of invasion from surrounding stands during the second year of the outbreak renders accurate prediction almost impossible. The only really practical method of dealing with these cases appears to be to treat the occurrence as a state of emergency and concentrate on preventing an outbreak in the first year.

6. Suggested Control Measures.

(1) *In Young Plantations.*

The initial source of beetle infestation in young pine plantations may be either the stumps of trees forming a previous crop, or an invasion from surrounding areas. The continuation of the insect population from a former crop occurs most frequently in the case of *Hylobius* and *Hylastes*, and these species may cause great damage to the young crop in its very early stages. Further investigation will be necessary before it is possible to deal successfully with the control of *Hylobius* and *Hylastes*, but reference will be made to these species when discussing the pole stage.

Infestations of *Myelophilus* need not arise in young plantations in Britain as a result of beetles breeding in the bark of old stumps within the area if the trees are cut off within a few inches of the ground. This reduces the risk of *Myelophilus* development in the stumps to a minimum. It may then be concluded that the infestations of *Myelophilus* arise through the invasion of adult insects from surrounding stands, and this generally takes place as soon as the trees are a few feet high. In order to prevent this invasion, it will be necessary to control the development of the *Myelophilus* populations in the surrounding areas.

Probably the most frequent source of infestation in young plantations occurs through piles of breeding material, in the form of thinnings, being left lying along the edges of neighbouring stands, or along the rides, or in other open places. The most severe invasions take place when a neighbouring stand is felled and the timber is left lying and beetles are allowed to breed in the bark and emerge in large numbers. These beetles immediately disperse throughout the surrounding area and feed in the shoots of the nearest pines. Much serious damage may be caused to young pines in this way, even before they reach the thicket stage, notwithstanding the fact that there may not be any available breeding material actually within the area.

In planting or regenerating sand dune areas, great care should be taken to avoid the use of pine thinnings or lop and top that includes any thick bark, for " thatching " dunes and moving sand. It must be remembered that a few acres of this material may attract large numbers of pine beetles from neighbouring stands, and although the material may not produce many young beetles per pair of parent beetles, the regeneration feeding of the parent beetles coupled with the feeding of the total number of young beetles may cause considerable damage to the nearest young pines growing in the locality.

Great care should also be taken to avoid planting pines on spots which are liable to be periodically flooded, or where the ground is likely to become waterlogged, as these spots will, sooner or later, become centres of infestation in which pine beetle populations rapidly develop in trees which are rendered unhealthy because of the unsuitable environmental conditions.

Observations made during the last few years in numerous young pine crops growing on various types of situation, in nearly every part of Great Britain, indicate that, from the viewpoint of insect control in pine areas, wide spacing of young plants is false economy, and close planting is of the utmost importance, particularly in connection with the control of pine beetles and pine shoot *Tortrix*, and the reduction of damage caused by these insects. When possible it is a great advantage to secure a dense crop of natural regeneration.

(2) *In the Early Pole Stage.*

In the case of Scots pine crops growing at fairly high elevation on poor soils, little attention is required during the first 30 years. But in the case of crops growing at low elevation on fairly deep soils, the position is entirely different, particularly if the trees were planted wide apart and have suffered heavily from the attack of pine shoot *Tortrix*. In these areas regulation of the crop, both as regards distribution of the trees and rate of growth, is of the utmost importance from the point of view of the future control of the bark-beetle population. Large crowned, and badly deformed trees with multiple leaders, which threaten to crowd out several smaller trees, should be removed as early as possible. The removal of these " wolf " trees will have the effect of reducing the general level of height growth of the crop, but will result in the maintenance of a higher average density, and the remaining trees will be more even in size. Maintenance of the average density, and the establishment of uniformity of the rate of growth of such a crop during the early stages is of supreme importance, and none of the smaller trees that are alive should be removed at this stage. The wolf trees should be completely trimmed out and the lop and top and material under 3 inches in diameter cut into short lengths so that it will lie close to the ground and thus hasten its decay and incorporation with the forest humus.

The time of year at which this pre-thinning treatment is carried out is of little importance, but it must be remembered that if the work is carried out during the winter or early spring, the presence of the fresh cut material will attract *Myelophilus, Hylastes, Hylobius* and *Pissodes* from surrounding pine areas early in the season. It will, therefore, be necessary to utilise the "wolf" trees as trap billets to prevent these insects from attacking the suppressed trees which have been left standing in the plantation. The butt length of each pole should be cut to a length that can be utilised subsequently. The remaining part of the pole down to 3 inches diameter should be cut into billets 2–3 ft. in length. These smooth-barked billets should be half buried in a flat position near the edge of the plantation in spots cleared of vegetation. The butt length will attract *Myelophilus* and *Pissodes* and the half-buried billets will attract *Hylobius* and *Hylastes*. The whole of the billets should be left *in situ* undisturbed until about the middle of May. They should then be barked and the bark left on the ground. The bark should not be burned, as this is a waste of time, and results in the destruction of the predators which will be present in large numbers. *Hlyobius, Pissodes, Hylastes* and *Myelophilus* adults found with the billets should, of course, be destroyed when the billets are being barked. It will be advisable to lay down a few more billets to attract any beetles that escape. About one set of billets for every ten sets laid down in the spring will be sufficient for this purpose.

(3) *During the Advanced Pole Stage.*

The proper disposal of thinnings is of great importance in the control of bark-beetles. If the thinning is carried out during the winter and early spring large number of bark-beetles are attracted from the surrounding pine stands. These beetles breed in the bark of the felled poles. In order to prevent a severe infestation, it will be necessary to bark all material over 3 inches in diameter before the end of May in order to destroy the broods before they become fully developed. It is not necessary to burn the bark, in fact this is undesirable, as it results in the destruction of the predators. It is quite unnecessary to bark smooth-barked material under 3 inches in diameter, and any unsaleable material of this size may with safety be left lying in the forest together with the lop and top without risk of a severe bark-beetle infestation. It is in fact an advantage to leave this material in order that it may become incorporated with the forest humus and thus help to maintain the fertility of the soil and improve its mechanical properties. Observations indicate that the disintegration of the material can be accelerated if it is cut into small pieces, and there is less risk of insect development of all kinds. The axil of the branch or point of juncture with the stem is one of the most favourable breeding places for many species of insects. Tops should therefore be trimmed out and should not be left lying intact.

Thinning experiments have shown that it is an advantage to delay thinning operations until after the breeding season of *Myelophilus*. If the thinnings are carried out during July, August and September, there is no risk of *Myelophilus* attack but the poles are liable to be attacked by *Pissodes*. However, this will not result in serious consequences if the poles are barked before the end of the following March. It will be seen, therefore, that thinning from July onward until October allows a much longer period for the removal of produce or for barking the material. It is important to see that all the drains are kept clear of litter, and it is essential at all times to keep them cleaned out and thus prevent waterlogging of the soil, for waterlogged soil causes trees to become sickly; these trees are then particularly susceptible to the attack of bark-beetles and weevils. If wet spots are found to occur, steps should at once be taken to drain the ground. Special attention should at all times be paid to windfalls and snowbreaks. These should be utilised as traps for bark-beetles. If the beetles are allowed to breed in this material it should be barked before the end of May. In north-east Scotland windfalls and particularly snowbreaks appear to be the chief breeding places for *Myelophilus minor*.

A very effective method of destroying large numbers of *Hylobius* and *Hylastes* larvae is to detach the bark of stumps a year after the thinning has taken place. If these insects are at all numerous in the area the bark on the stumps will by that time have become thoroughly infested and can be detached quite easily with a large chisel, a barking iron or notching spade. Barking fresh stumps is quite useless and is a waste of time and only attracts the insects which then breed in the bark of the roots.

If *Myelophilus* is found to be increasing in pole plantations, and billets are used to trap the beetles, trees which show signs of beetle attack should be utilised for this purpose. These trees can readily be detected by the presence of resin blobs in the crevices of the bark, but if any windfalls occur these should be utilised for the purpose. Cutting down fresh trees only adds to the available amount of breeding material and helps to relieve any overcrowding that would otherwise take place in suppressed or dying trees which may be present in the stand.

Control measures in felling, burnt and windfall areas were discussed in a previous paper.

7. Need for greater Attention to Forest Entomology.

The foregoing observations indicate that many injurious forest insects have become of greater importance in Britain during recent years, both as regards increase in numbers and geographical distribution, and it is safe to predict that with the increase and development of the forests in this country the risk of serious insect outbreaks will be enormously increased in the near future. Examples have been given to show how insect outbreaks may arise through failure to understand the rudimentary principles underlying the development of insect populations. Sufficient attention has not been paid to the first-hand study of forest entomology in Britain, and the urgent necessity for a detailed survey of forest insects, and an extensive increase in the facilities for original research cannot be too strongly emphasised. Control methods should not consist of waiting until insects reach pest proportions, and then concentrating on devices for their destruction. Modern methods must be directed to the prevention of damage. This can only be attained by controlling the insect populations at a low level of density, and will necessitate a more comprehensive study not only of the habits of the insects directly concerned but also of their parasites, predators and other natural enemies, and the various ecological factors which govern their existence and increase. J. F. V. Phillips (1931) emphasized the fact that ecology is the foundation of forestry and defined ecology as " the study of the inter-relations of plants and animals and their environments, and for forestry purposes as the study of communities of plants and animals as regards their origin, development, function, responses, reactions and management. That forest ecology takes cognisance of animals as well as of plants, is intimately concerned with the coactions among animals and plants, and with the inter-relations of animals, plants and physical factors, must be emphasised for the reason that in the minds of many foresters and botanists forest ecology embraces the study of plants and plant communities only." Dr. Phillips very truly stated that " the older forest pathology taught as golden rules the cutting and burning of infested material, the collection of fructifications of the larger fungi, the destruction of insect imagoes, larvae and where possible eggs. It paid little attention to the fundamental truth that prevention is better than cure. The whole emphasis so far as the pathologist was concerned was upon the organism causing the disease, while the forester concentrated upon the removal of diseased material." Unfortunately this is not entirely a thing of the past, although during recent years many workers in economic entomology have become convinced that the correct procedure is to control the injurious insects at a level of density below that at which economic damage occurs. This point of view requires a certain amount of imagination, and many persons prefer to expend funds on the destruction of insects that have caused enormous damage, rather than on the prevention of destruction, however inevitable that destruction may be if the necessary steps are not taken to control the insects. In discussing insect pests, the following statement was made in the Annual Report of the Intelligence Division of the Board of Agriculture and Fisheries (1908) : " The State has been frequently recommended to take upon itself the cares and duties of afforestation, and estimates have been made of the profits likely to accrue to subsequent generations by the timely action of the present one. In most of these estimates no definite depreciation has been allowed for on account of such pests as the one under discussion, but if the State is to take over the work, now left undone by private landowners, of increasing the area of British soil under forest management, it will be more than ever bound to devote its attention to such possible and even probable sources of loss as insects and fungus pests, and to insist in self defence that private landowners shall not permit the unchecked development of these parasites which would certainly spread to and eventually render valueless the property of the Government." Apparently the official who wrote the above failed to appreciate the fact that the landowners to whom he referred, together with the other members of the community, constitute the State and are the joint owners of the forests which require to be protected, and that the majority of these individuals are anxious to see both State and private forests protected from the ravages of insect pests. Having, however, appointed experts to carry out a policy of forest conservation, they expect the men entrusted with this task to see that proper precautions are taken to protect the forests. Many private forest owners are anxious to control destructive insects and regard it as the duty of the State to provide advice and the necessary facilities which would enable them to do so. It must be admitted that there is something to be said for their point of view. In spite of the fact that the value of forest crops in Britain amounts to many millions of pounds, no facilities exist for the provision of entomological advice to forest owners, although extensive facilities exist for agriculturists. This neglect of attention to forest entomology, if continued, will undoubtedly result in heavy financial losses and the situation cannot be regarded with equanimity.

In order to ascertain how the insects are to be kept under control it is necessary to find out what are the factors that normally limit their increase. The proper time to collect evidence of control is during the period when control is actually in operation. Once the balance has been upset and conditions have become favourable for the rapid increase of any particular species of insect and it has become a pest of great importance, there is little opportunity to study the normal relationship of the insect and its environment and in addition to heavy expenditure on control measures, the situation is aggravated by the fact that this expenditure is chargeable to the upkeep of a devastated crop.

Maximum opportunities for the successful employment of biological control measures occur in silviculture. Forest crops generally occupy the same soil and situation for a long period of years and the crops are chiefly grown on land which is, for a variety of reasons, unsuitable for agriculture. In most cases the crops are grown at fairly high elevation and to a great extent provide their own shelter. In many cases they cover very large areas, and during the thicket stage, which often extends over a period of many years, they are to a large extent impenetrable and detailed examination is extremely difficult, so that facilities for the undetected development of insect populations reach their maximum. Mistakes made in the establishment of the crop cannot be rectified from year to year, as in the case of agricultural crops. Trees which are growing on unsuitable soils or in unfavourable situations are liable to become unhealthy and are predisposed to the attack of insects and fungi. Insect damage may be of various kinds and may result in either loss of increment, or of height growth ; in malformation of the stem ; in reduction in the quality of the timber ; or in the premature death of the tree. Damage caused during any particular year may not appear to be of any great importance, but it must be remembered that in the case of forest crops the effects of damage from year to year are cumulative and in the aggregate the combined effects of several attacks may result in a great reduction in the value of the produce and consequently in great financial loss.

During recent years great efforts have been made in various parts of the world to deal with forest insect pests by means of chemical treatment on a large scale by the use of aircraft and other mechanical devices, but the experiments cannot be said to have been very successful. These methods can only be applied to leaf-eating insects and only under certain conditions. There are many serious objections to these forms of wholesale chemical treatment, and it is conceivable that persistence in their use might result in very harmful repercussions in many directions. Chemical treatment on a small scale, where the material used can be controlled, may sometimes be utilised with advantage, but its cost is, as a rule, prohibitive. Mechanical methods of control, such as trapping and collecting, have for many years been extensively used in connection with the control of certain species of forest insects. They are very expensive and are a recurring charge and cannot be entirely relied upon to keep the insects in check, and although these methods, which are useful in dealing with certain species on a small scale, will probably always have a place in any complete system of insect control measures, it will always be necessary to curtail their use as much as possible on financial grounds.

Cultural methods of control in forestry have in the past received little attention but it is becoming increasingly apparent that they are of considerable importance and form an inseparable part of all biological control work. In order to carry out successfully any work in biological control it is not only necessary to investigate thoroughly the ecological factors governing the existence of the host insect and its parasites and predators, but it is equally necessary to understand thoroughly the ecological factors associated with the growth and successful development of the host plant or plants concerned. The forest entomologist must be able to form a fairly accurate idea as to whether a crop is making satisfactory growth under any particular set of conditions with which it is associated and be able to decide what factors are responsible for any unsatisfactory state in the health of the crop as a whole, or of any of the trees in the crop. The more or less permanent character of the forest crop provides maximum facilities for the development of a very diverse insect population which is also of a somewhat permanent character, and it is that state of continuity in the insect population and its environment that provides unique opportunities for the application of biological control in dealing with forest insects. Some species of insects are directly associated with the trees forming the forest crop, others are associated with various species of plants which become established in the area. Little is known about the feeding habits of many of the forest insects in the adult stage, particularly the parasitic insects. This is a subject of the utmost importance and an investigation of the food-plants of the adult parasites is urgently needed in order to ascertain how the work of the parasites can be facilitated and their efficiency increased. Much work also remains to be carried out in connection with the study of host-plants for the various species of insects which act as alternative hosts for the parasites of the insects which attack the trees. J. W. Munro (1931) admirably emphasises the importance of this aspect of the subject in the following words : " Numerous instances can be given to show how the forest vegetation has an important indirect bearing on the forest pest and it is because of this complex inter-relationship of pest and parasite, parasite and alternative host, and alternative host and the forest vegetation, that parasite control as applied to forest insects is both so fascinating and so difficult.

"The forest floor vegetation depends partly upon soil conditions and partly on the type of forest itself ; that is to say, on silvicultural practice. Accordingly we find ourselves once more faced by the fact that in considering the use of parasites we cannot ignore silvicultural practice. In other words, in biological control by parasites, as in all other methods of insect control, there is the closest relationship between the methods to be employed and the methods of silviculture, and it is conceivable that in the application of control by parasites of forest insect problems we may yet have to consider and to investigate the whole question of the effects of silvicultural practice on the forest insect fauna.

"The fact that much biological work has to be done before we understand the relationship of silvicultural practice to the forest insect fauna in no way detracts from the value of parasite control. Parasite control, like forestry itself, is slow in yielding returns, but there is no doubt that ultimately this method, both directly and indirectly, has the utmost value in forest biology. In fact it may be that the study of control of forest insects by parasites will lead to a fuller understanding of silviculture itself."

8. Summary and Conclusions.

1. This is an account of the continuation of experiments and observations carried out in connexion with an investigation into the ecology and control of pine beetles in Great Britain, with special reference to *Myelophilus piniperda* and *M. minor*.

2. The nature and scope of the investigation is described and attention is directed to the necessity for studying not only the factors which govern the interaction of the injurious insects and their parasites and predators, but also the ecological factors associated with the host-plant. In fact, the host-plant is regarded as the centre of the problem.

3. Reference is made to the earlier experiments and a brief outline is given of the results obtained. Subsequent experiments are described in detail. The results of these later experiments, which were carried out on a much larger scale and on a wider basis, confirm the results obtained in the earlier experiments, and show that in carrying out thinning operations in Scots pine areas it is quite safe to leave thin-barked material of small diameter lying on the ground without risk of causing a bark-beetle outbreak, and it is shown that in addition to considerable saving in expenditure, this procedure is beneficial to the crop and provides for the maintenance of a permanent population of parasites and predators.

4. The results of thinning in summer instead of during the winter are described in detail, and it is shown that the risk of causing a bark-beetle outbreak is less when thinning is carried out during the summer, and that a longer period for dealing with the material is provided. Certain precautions are, however, necessary to prevent an increase in the *Pissodes* and *Hylobius* populations.

5. The results of the billet and trap stem experiments show that standing trap stems cannot be relied upon to give consistent results. Felled stems were found to be much more reliable, but where trapping is considered to be necessary the use of billets is to be preferred. The manner in which they should be prepared is described.

6. Attention is directed to the importance of windfalls and snow-breaks in providing facilities for the increase of bark-beetles, particularly in the case of *Myelophilus minor* in north-east Scotland, and the necessity of utilising this material for bark-beetle control purposes is emphasized.

7. An outline of the results of the recent bark-beetle survey is given. These results indicate that there has been a considerable increase in the geographical

distribution of various species of bark-beetles in Britain during recent years, and that certain species which were formerly regarded as rare insects have now become quite abundant. Other species, of which individual specimens have occasionally been recorded as introductions, are now thoroughly established as resident breeding species. Evidence is produced which indicates that one of these species has for a number of years been a pest of considerable importance.

A list of bark-beetles which are imported into Britain in the bark of pit props is given. These insects were found emerging in thousands from material loaded in railway trucks consigned to South Wales collieries. Some of these species which have not hitherto been regarded as British were found breeding in pine crops in South Wales and the south of England. It is pointed out that although the importation of these bark-beetles may have been a matter of little importance while South Wales was destitute of coniferous forests, the position will be quite different now that coniferous forests are being developed in that area.

8. Bark-beetles of the genus *Hylastes* were found to be very numerous in many parts of the country, and in addition to causing destruction in young plantations, they were found to be killing pines in the pole stage and also mature trees. Examples are given of cases where *Hylastes* and *Hylobius* were found to be killing pines 15 years of age by attacking the roots for breeding purposes. *Hylobius* is considered to be the most destructive forest insect in Britain at present, and it is extremely abundant in pine areas where extensive felling is taking place, particularly in Scotland. *Pissodes notatus* was also found to be doing considerable damage in young plantations in England, Corsican pine being particularly susceptible to the attack of this species.

9. *Myelophilus piniperda* was found to be considerably more numerous in England than in Scotland in proportion to the areas of pine forest. *Myelophilus minor* appears to be extending its range of distribution and was found to be very numerous in some parts of north-east Scotland.

Although it is considered that none of the bark-beetles need become serious pests in Britain if proper precautions are taken to keep them under control, examples are given of recent outbreaks which have occurred in this country, and it is shown that in each case the outbreak was a result of mismanagement and lack of understanding of the biological principles underlying the control of insect populations.

10. The development of bark-beetle populations is discussed, and it is shown that various factors influence the rate of reproduction of the adult insects ; and that the density of the population steadily increases with the increase in density of the stand and also with the advance in age of the crop, until the period of maximum density is reached. The density of the bark-beetle population then decreases. Under normal conditions the population is controlled at a low level of density by the combined action of a number of factors which are discussed in detail. Examples are given to illustrate how this control is maintained under normal forest conditions, and the importance of parasites and predators is emphasised.

Abnormal conditions result in a rapid increase in the bark-beetle population and if unchecked the beetles cause serious damage.

The intensity of a bark-beetle outbreak depends on the amount of suitable breeding material and on the density of the initial population when facilities for increase occur. It is therefore of the utmost importance that the bark-beetle population should be kept at a low level of density. Stress is laid on the importance of preventing outbreaks rather than on destroying mature insects which have been allowed to develop.

11. Measures for the control of bark-beetles during all stages of the crop's development are discussed.

12. The urgent necessity for greater attention to the study of forest entomology is pointed out, and it is suggested that greater facilities should be provided to

encourage and assist owners of forests to control insect pests. Provision should also be made for increased facilities for research, particularly in connexion with the biological control of forests insects.

9. Acknowledgments.

The writer desires to thank the numerous landowners who so readily showed their willingness to co-operate in the work and gratuitously provide the desired facilities ; the Forestry Commission for making the investigation possible ; the members of their staff, and the factors, land agents and foresters who so enthusiastically helped forward the work ; the various members of the staffs of the Natural History Museum and the Imperial Institute of Entomology for the identification of specimens, and assistance in translating the foreign literature ; and all others who have in any way helped to complete the task.

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EXPLANATION OF PLATE XVII.

Fig. 1.—A 48-year-old Scots pine plantation after thinning. The density is 550 stems per acre. This stand had not previously been thinned. All the thin-barked material was left lying on the ground as seen in the photograph. The number of fallen shoots in this area was less than 1 per square yard throughout the following autumn and winter.

Fig. 2.—Part of a root attacked by *Hylastes ater*. A portion of the outer layer of bark has been removed to show the adults feeding in the inner bark (× 2½).

Fig. 3.—Part of another root with the bark removed to show full-grown *Hylobius* larvae which have been feeding under the bark. The round hole is the entrance to the pupal chamber in the wood. (Diameter × 2.)

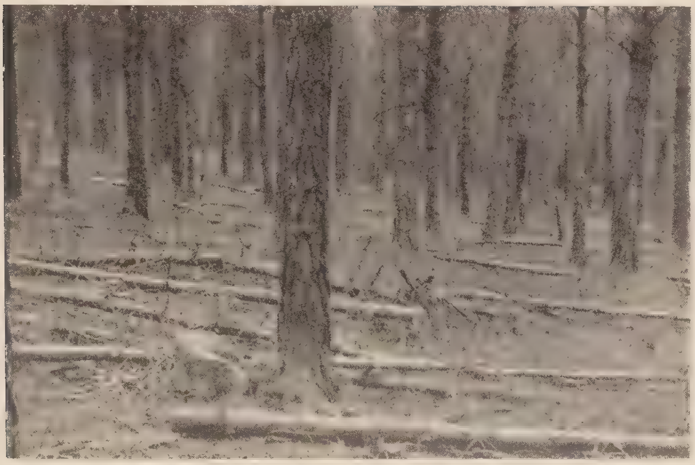

Fig. 1.

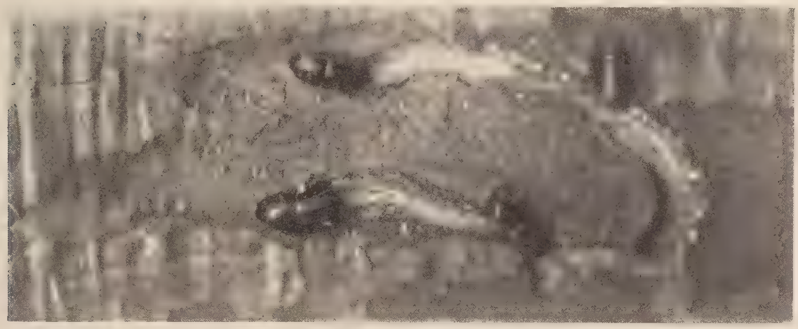

Fig. 2.

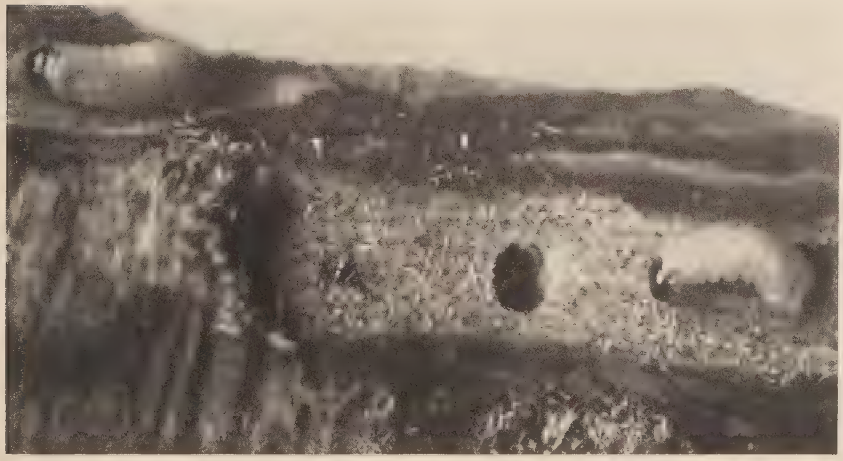

Fig. 3.

EXPLANATION OF PLATE XVIII.

The results of careless extraction of thinnings. Large patches of bark have been torn from the base of many of the trees left to form the final crop. This allows access of injurious insects and fungi and causes the premature destruction of the trees.

EXPLANATION OF PLATE XIX.

Part of a 35-year-old Scots pine plantation which has recently been thinned. This stand had not previously been thinned and was very dense. The crop has been heavily overthinned and large numbers of dead, dying and badly suppressed trees have been left standing. These trees form suitable breeding material for *Myelophilus* and other injurious insects.

NOTES ON THE VARIEGATED GRASSHOPPER, *ZONOCERUS VARIEGATUS*, L., IN NIGERIA.

By F. D. Golding, M.A., F.R.E.S.

The object of the present paper is to describe the results of some cage experiments with *Zonocerus variegatus*, L., carried out at Ibadan between March 1932 and December 1937.

The cages used for the breeding experiments were about 2·05 metres in height and were filled with soil to a depth of about 51 cm. The upper part of each cage was made of wire gauze and had a cubic capacity of about 1·43 cubic metres (154 cm. high by 102 cm. by 91 cm.). The grasshoppers were fed on the leaves of sweet cassava (*Manihot utilissima*) and water was sprinkled on the food.

Distribution.

Z. variegatus is widely distributed in the Southern Provinces of Nigeria and has been recorded from a number of localities in the Ilorin Province, Gadau (Bauchi) and the vicinity of Lake Chad in the north. According to Chevalier[1] this species occurs in the coastal zone from Senegal to the south of the Gulf of Guinea ; there are also records of its occurrence in the Gambia, French Sudan and the Colonie du Tchad. *Z. variegatus* ranges across Tropical Africa through the Belgian Congo to Uganda and Kenya.

Food-plants.

The Variegated Grasshopper is remarkably polyphagous and amongst its local food-plants may be mentioned cotton, cassava, maize, cacao, kola, cowpeas, bananas and citrus.

Migration.

The larvae are gregarious and have been observed, in some years, to migrate for considerable distances. Hargreaves[2] has recorded that in Sierra Leone there is a general easterly movement of the hoppers and that towards the end of the dry season there is a migration in the reverse direction, which indicates that the insect returns to its original breeding ground. A similar easterly movement of hoppers has been observed on several occasions at Ibadan ; but no evidence of a return migration has been obtained. In 1922 *Zonocerus* larvae were unusually abundant at Ibadan and migration was rapid ; as a rule, the movement is gradual.

Cage Experiments.

In December 1938, in order to compare the climatic conditions inside the cages with those outside, maximum and minimum and wet and dry bulb thermometers were set up in one of the cages, the roof of which was then covered with palm fronds. The readings were compared with those recorded by identical instruments under a thatch-roofed hut about 100 yards from the cage. The differences between the various readings, viz., maximum and minimum shade temperatures and morning and afternoon relative humidity, taken in the cage and hut were insignificant.

It was then decided to compare the evaporative power of the atmosphere inside the cage and in the open by means of Livingston standardized white spherical atmometers. Accordingly, the palm fronds were removed from the top of the cage and, during 20 rainless days in February 1939, evaporation was recorded by means of three atmometers in each locus. The mean quantity of water lost *per diem* in the open was 36·1 c.c., while in the cage the amount evaporated was only 26·5 c.c., or 26·6 per cent. less.

During February 1939, comparative readings in cage and open were made by means of a black bulb thermometer *in vacuo*. It was found that the mean daily difference between maximum temperature in the cage and open was 35°F.; this represented a reduction of 23·8 per cent. in the cage maximum temperature as compared with that in the open. It is evident that the wire gauze sides and top of the cage cut off sunlight very considerably, with the result that the temperature of the air inside the cage was lower than in the open during the daytime. This shade effect was also responsible for reducing the evaporative power of the air inside the cage.

Life-Cycle.

In March 1932, 144 adult *Zonocerus* were collected in the field and placed in cages of the type described above. Between that month and March 1937 there were five generations, or one *per annum*. The first and last dates on which copulation was observed, the first date on which oviposition was seen and the dates of hatching and final ecdysis are shown in Table I.

TABLE I.

	1932	1933	1934	1935	1936
Copulation :—					
First seen ...	March 15	April 6	April 3	March 18	March 20
Last seen ...	June 20	June 18	May 4	—	July 10
Oviposition ...	April 6	—	April 7	April 12	April 23
Last adult died ...	July 4	July 22	July 28	July 31	Aug. 25
Hatching	Oct. 21, 30 Nov. 1	Oct. 18, 24 Nov. 6, 27, 29	Oct. 31 Nov. 9, 16	Oct. 30 Nov. 9, 14	Nov. 2, 4, 7 9, 12, 16
Final ecdysis (first adult)	Feb. 2 (1933)	Jan. 30 (1934)	Feb. 6 (1935)	Feb. 17 (1936)	Mar. 5 (1937)

There was a considerable degree of uniformity in the sequence of events during the first four years. The shortest period between hatching and final ecdysis was 104, 104, 98 and 110 days in 1932, 1933, 1934 and 1935, respectively. The average minimum duration of the five larval instars during those four years was as follows: 14, 20, 23, 25 and 22 days.

Field observations at Ibadan showed that hatching usually took place at about the same time in the field as in the cages, except that at least one batch of eggs must have hatched in mid-September 1933 and that, in 1936, eclosion occurred between about the 6th and 21st October. Final ecdysis began about a fortnight earlier in the field than in the cages. On the other hand, there is evidence that occasionally hoppers hatch in the spring at Ibadan; this subject is discussed later in the paper.

Climatic Conditions and Sexual Maturation of the Adults.

The mean maximum shade temperature, mean relative humidity at 9 a.m. and 3 p.m., and rainfall for various weekly periods between 1932 and 1936, are shown in Table II.

TABLE II.

Week ending	Mean maximum temperature, °Fahr.	Mean relative humidity at 9 a.m. per cent.	Mean relative humidity at 3 p.m. per cent.	Rainfall in inches	No. of days on which rain fell
1932					
Feb. 29 ...	93·0	81·4	58·3	0·00	0
Mar. 7 ...	90·4	82·6	68·5	0·86	4
,, 14 ...	**91·6**	**86·6**	**72·6**	**2·24**	2
,, 21 ...	91·1	80·4	69·4	1·10	2
,, 28 ...	90·4	84·1	73·8	1·70	5
1933					
Mar. 7 ...	91·1	84·6	65·1	0·84	1
,, 14 ...	90·6	85·5	67·6	0·30	1
,, 21 ...	91·3	83·6	59·7	0·46	1
,, 28 ...	90·4	81·8	64·5	3·19	2
April 4 ...	**91·1**	**80·1**	**65·8**	**2·38**	2
,, 11 ...	89·7	81·7	68·1	0·01	1
1934					
Mar. 7 ...	93·1	81·0	51·4	0·00	0
,, 14 ...	90·9	81·6	49·1	0·72	2
,, 21 ...	92·2	84·8	57·7	1·81	3
,, 28 ...	90·2	85·6	62·9	1·25	3
April 4 ...	**89·3**	**89·1**	**74·9**	**3·44**	3
,, 11 ...	89·0	90·4	75·9	0·90	3
1935					
Feb. 28 ...	92·7	80·5	49·0	0·14	2
Mar. 7 ...	94·8	75·5	40·9	0·18	2
,, 14 ...	91·4	75·9	50·3	0·07	1
,, 21 ...	**89·0**	**82·4**	**60·1**	**4·74**	3
,, 28 ...	90·7	84·1	58·6	1·27	2
1936					
Feb. 29 ...	91·7	82·6	65·0	0·60	2
Mar. 7 ...	88·7	82·3	65·9	1·14	1
,, 14 ...	90·1	83·5	58·7	0·03	1
,, 21 ...	**91·9**	**78·5**	**59·4**	**0·91**	1

Fluctuations in the mean temperature for the weekly periods shown in Table II were comparable to those in the mean maximum temperature.

From Table I it will be seen that the dates on which copulation was first observed were 15th March, 6th April, 3rd April, 18th March and 20th March, in 1932, 1933, 1934, 1935 and 1936, respectively; records for the nearest date in Table II are in clarendon. The record for 1933 should be regarded with suspicion, for the absence from Ibadan at that time of the writer and two of his assistants made it necessary to entrust the observations to an unreliable observer.

It is evident that sexual maturation of the adults is correlated with the onset of the rains and the concomitant increase in atmospheric humidity. In 1932, 1934 and 1935, the humidity was increasing in the fortnight preceding the date on which copulation was first observed.

In the Chad area (north-eastern Nigeria) *Zonocerus* hoppers have been observed in May and June and a worn adult was collected on 10th October, 1931. Large hoppers and recently-emerged adults were received from Gadau (Bauchi Province) in early August 1937. It is evident that in these northerly areas eclosion takes place during April and sexual maturation in late August or early September. In these areas about 75 per cent. of the total rainfall falls between 1st July and 15th September, and it is only during this period that the humidity reaches 80 per cent. at 9 a.m. and 60 per cent. at 3 p.m. Meteorological observations made by Mr. A. M. Gwynn near Lake Chad in 1934 show that the mean relative humidity was 72, 81 and 72 per cent. at 9 a.m., and 51, 67 and 53 per cent. at 3 p.m. in July, August and September, respectively.

Climatic Conditions and Hatching.

The eggs of *Z. variegatus* are deposited at a depth of about three inches below the surface of the soil. No data are available showing soil moisture and temperature at that level; it seems improbable that changes in atmospheric humidity can have a marked effect upon the moisture content of soil three inches below ground-level. The amount of precipitation would appear to be the best available index of soil moisture conditions.

The mean maximum shade temperature and the rainfall for various weekly periods from 1932 to 1936 are shown in Table III.

TABLE III.

Week ending	Dates on which hatching occurred	Mean maximum temperature °Fahr.	Rainfall in inches	No. of days on which rain fell
1932				
October 7	—	84·0	1·25	5
,, 14	—	86·6	2·54	5
,, 21	Oct. 21	**83·1**	**0·90**	3
,, 28	—	83·7	1·26	4
November 4	Oct. 30, Nov. 1	**86·9**	**0·61**	4
1933				
October 7 ...	—	83·9	2·01	6
,, 14 ...	—	84·7	3·32	7
,, 21 ...	Oct. 18	**87·9**	**1·40**	3
,, 28 ...	Oct. 24	**88·4**	**0·65**	2
November 4 ...	—	86·1	1·86	5
,, 11 ...	Nov. 6, 27, 29	**84·8**	**1·29**	3
1934				
October 7 ...	—	84·8	2·58	3
,, 14 ...	—	85·1	1·45	3
,, 21 ...	—	85·2	1·40	2
,, 28 ...	—	83·8	0·82	4
November 4 ...	Oct. 31	**86·5**	**1·41**	4
,, 11 ...	Nov. 9	**87·5**	**0·18**	1
,, 18 ...	Nov. 16	**88·2**	**0·00**	0
1935				
October 7 ...	—	85·7	0·82	3
,, 14 ...	—	84·8	0·05	1
,, 21 ...	—	85·8	2·50	4
,, 28 ...	—	86·8	0·95	4
November 4 ...	Oct. 30	**85·0**	**0·54**	2
,, 11 ...	Nov. 9	**87·0**	**0·24**	2
,, 18 ...	Nov. 14	**87·7**	**0·00**	0
1936				
October 7 ...	—	84·9	2·27	4
,, 14 ...	—	84·9	0·34	3
,, 21 ...	—	88·1	0·65	3
,, 28 ...	—	88·3	1·74	2
November 4 ...	Nov. 2, 4	**89·0**	**0·98**	3
,, 11 ...	Nov. 7, 9	**88·4**	**1·34**	5
,, 18 ...	Nov. 12, 16	**87·2**	**0·31**	2

The mean maximum shade temperature for the month of September was 81·0, 83·1, 84·5, 82·3 and 81·2°F., in 1932, 1933, 1934, 1935 and 1936, respectively. It will be seen that in every week, except that ending on 28th October, 1934, the maximum temperature exceeded the September mean for the corresponding year. In each year, hatching did not occur until the mean maximum temperature had reached 86·5°F. It is obvious that the temperature of the soil surrounding the egg-mass is largely dependent on the amount of moisture it contains. It seems probable that the combined effect of the increase in air temperature and the slackening off of the rains in the second half of October resulted in an increase in the temperature of the soil surrounding the eggs and thus induced eclosion.

Van der Merwe & Kent[7] have recorded that, in South Africa, the eggs of the closely-related *Zonocerus elegans*, Thnbg., usually hatch after rain; but they quote an instance of eclosion taking place during the dry weather when there was not even dew at night.

On 16th May, 1935, the writer found a band of 3rd instar hoppers on the bank of the Chari river near Fort Lamy. Hatching must have occurred in early April or more than a month before the beginning of the rains in that locality. O. B. Lean observed that, near the Niger in French Sudan, hatching took place in early May before the beginning of the rains.

In the Chad area, the mean maximum temperature rises from 87°F. in January to 108°F. in April; there is heavy dew at night in January and February and little or no dew in April, when eclosion takes place. It seems probable that in the north the soil surrounding eggs which ultimately hatch is very moist on account of its proximity to water, and that the soil temperature required to induce eclosion is not reached until the air temperature is considerably higher than at Ibadan in October.

Soil Aridity and Oviposition.

Experiments in which egg-masses deposited in damp soil in April were transferred to dry soil always resulted in the eggs becoming shrivelled and failing to hatch.

On 25th March, 1935, ten pairs of adults were placed in a cage containing dry soil. On 3rd, 18th and 24th April, egg-masses were found attached to the wire gauze sides of the cage and, on 5th July, a female deposited eggs on a cassava leaf. The last adult died on 31st July, and examination of the soil showed that it contained only one very small batch of shrivelled eggs. The soil was loose and could easily have been penetrated by the abdomen of an ovipositing female.

In 1936, copulation began on 20th March in the main experimental cages; but except for one egg-mass deposited on a leaf on 15th April, oviposition did not begin until 23rd April. A heavy shower of rain on the 22nd had thoroughly moistened the soil, and thirteen females were observed ovipositing on the following morning.

TABLE IV.

Cage No.	Date of oviposition	Date of hatching	No. of hoppers hatched	Incubation period in days
	1937	1937		
2	16th May	26th November	12	194
21	14th June	21st December	8	190
		22nd December	1	191
22	2nd July	28th December	29	179
29	30th June	18th December	10	171

Between 14th April and 15th June, 1937, thirty-six pairs of copulating adults were placed in 36 small cages containing moist soil ; after oviposition had taken place the grasshoppers were removed. In twelve of the cages no water was added after the eggs had been deposited, in twelve water was added on every day on which rain fell, and in the remaining twelve water was added on six days of each week. No hoppers emerged from the eggs in the first two series of cages ; the amount of water added to the second series corresponded to the rainfall during the experimental period. Hoppers emerged from the eggs in four of the twelve cages where soil was watered six times a week. Table IV shows the dates of oviposition and eclosion and the number of hoppers hatched in each cage.

It is evident that soil moisture is an important factor during the incubation period.

There are twelve records of *Zonocerus* hoppers being found in the north, and in every instance they were either on the bank of a stream or in a low-lying marshy area. It seems probable that *Z. variegatus* can exist in the north only in special areas where proximity to water ensures that the eggs are kept moist during the incubation period.

Hatching in the Spring.

As stated above, hatching occasionally occurs in the spring at Ibadan. Three hoppers were found near a marsh in July 1923 ; twenty 1st instar hoppers were seen near a river on 11th February, 1939 ; one 2nd instar nymph was taken on the bank of the same river on 16th May, 1937 ; five 5th instar hoppers were collected in the field on 31st July, 1935 ; and one worn adult was seen on 7th December, 1938. The five 5th instar nymphs were placed in a cage ; four died during August, whilst the fifth, a female, completed her final ecdysis on 5th September, 1935. This female oviposited on 29th November, 25th December and 31st January ; on each occasion the egg-mass was small and was attached to the wire gauze side of the cage.

Peacock[6] states that "All stages of young were found towards the end of October 1911, at Ibadan, and, in March 1912, in the Central Province." The old Central Province consisted of the present Benin and Warri Provinces and parts of Ondo, Ogoja, Onitsha and Benue.

Lamborn[5] records that "Immense swarms of nymphs appeared suddenly, all about the same time in November," and that "The insects gradually scattered as they attained maturity, and in late January completed the last ecdysis . . . . . after which they were to be seen *in coitu* everywhere, and shortly afterwards new swarms of larvae appeared." From the above it appears that the spring hatching at Ibadan in 1914 was considerably greater than it has been in any spring during the writer's residence in Nigeria (1922 to 1939). It is possible that the spring-hatched larvae seen by Lamborn were not the progeny of the adults which became sexually mature in February 1914, but were derived from adults which became mature in the preceding autumn. The writer's discovery of 1st instar hoppers on 11th February, 1939, makes it seem highly improbable that, in this instance, the nymphs were derived from eggs laid in the spring. In the field, in 1939, final ecdysis was first observed on 3rd February and copulation on 18th February. Two possible explanations come to mind. Firstly, it was found in the cage experiments that oviposition took place over a period of about three months ; most of the egg-masses were deposited before the end of May. It is possible that the hoppers hatching at the normal time, viz., late October, are derived from the earlier-laid egg-masses and that the later-laid ova fail to hatch, unless they happen to have been deposited close to water. It will be remembered (Table IV) that hatching of July-laid eggs took place as late as 28th December in cages with thoroughly moistened soil. Secondly, it may be that there is a small population of *Zonocerus*, permanently resident in the vicinity of the river, whose life-cycle is chronologically similar to that of individuals occurring in similar loci in the north. It is hoped that future research will provide the explanation of this interesting phenomenon.

Spring hatching also occurs in other parts of the Southern Provinces. Ten 3rd and 4th instar nymphs were collected between 8th and 14th July, 1937, at Nkwele (near Onitsha) and many worn adults were seen at Umuahia (Owerri Province) on 21st September, 1935. Mr. J. W. Wallace kindly questioned local natives at Umuahia and was informed by them that adults are usually seen from late September to April. There seems little doubt that the worn adults, observed by the writer, were derived from eggs which had hatched in the spring.

In the Ilorin Province, spring hatching appears to be more frequent than eclosion in the autumn. In this area *Zonocerus* has been found only in marshes and near rivers or streams. The available data concerning the incidence of *Z. variegatus* in the Ilorin Province are shown in Table V.

TABLE V.

Locality	Date seen	No. seen	Instar
Ilorin	20th March, 1930 ...	Two bands ...	—
Omu Aran ...	24th April, 1937 ...	Small band ...	2nd
Ilorin	4th May, 1937	,, ,, ...	2nd
Oke Odde ...	7th May, 1937	,, ,, ...	2nd
Share	9th May, 1937	,, ,, ...	1st and 2nd
Balah	27th July, 1937 ...	Two	3rd
Oke Odde ...	13th August, 1937 ...	Three	3rd and 4th
Lafiagi	14th August, 1937 ...	,, ...	3rd and 4th
Balah	2nd November, 1937 ...	One	Adult
Ilorin	4th November, 1937 ...	Four	Adults
Esiye	6th November, 1937 ...	Small band ...	1st
Ajasse	22nd April, 1937 ...	One	Adult (recently moulted).

Hargreaves[3] records that, in Sierra Leone, hatching takes place from late September to late December, and in a later publication[4] states that " Some of the eggs hatched in one locality during April and May."

Mayné, quoted by Vayssière & Mimeur[8], records that in the equatorial region of the Belgian Congo eclosion takes place from mid-February to March, and that the adults copulate in September and October.

Summary and Conclusions.

1. Cage experiments were carried out at Ibadan between March 1932 and December 1937. There was one generation a year of *Zonocerus variegatus*. The adults became sexually mature in March or April ; oviposition began in April ; hatching took place in late October or November ; final ecdysis began between late January and early March. The average period between hatching and the final ecdysis of the first nymph was found to be 104 days.

2. Sexual maturation of the adults appeared to be correlated with the onset of the rains and the concomitant increase in atmospheric humidity. In the arid north, the adults become sexually mature during the only period in the year when the humidity at 9 a.m. reaches 80 per cent. and at 3 p.m. 60 per cent.

3. Hatching did not occur until the mean maximum shade temperature had reached 86·5°F. It was concluded that the combined effect of an increase in air temperature and the slackening off of the rains resulted in an increase of the temperature of the soil surrounding the eggs and thus induced eclosion.

4. It was demonstrated experimentally that the egg-masses are dependent on a high degree of soil moisture during the incubation period. It is thought that *Zonocerus* can exist in the north only in special areas where proximity to water keeps the eggs moist during the incubation period.

In conclusion, the writer wishes to express his indebtedness to Dr. Uvarov for helpful criticism.

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NOTES ON THE DISTRIBUTION OF *CEPHUS PYGMAEUS*, LINN., AND OF ITS PARASITE, *COLLYRIA CALCITRATOR*, GRAV.

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1. Introduction.

The wheat crops in certain districts of England are attacked every year by the wheat-stem sawfly, which in its turn acts as host to various species of parasitic insects. The aim of the present investigation is to try to discover from an analysis of records if any sort of simple numerical relations exist within the complex including the wheat field, the sawflies which infest the wheat-stalks, and the parasites which attack the sawflies. The results of this work lead to a discussion of the peculiar difficulties involved in the application of mathematics to the study of animals and plants in their natural environments.

This investigation is an extension of one which has already been made on the distribution of eggs by the Ichneumonid parasite, *Collyria calcitrator*, Grav., among the larvae of its host, the wheat-stem sawfly (*Cephus pygmaeus*, Linn.), namely the analysis of superparasitism (Walker, 1937). It is now proposed to study the relations between plant density, *Cephus* density, and parasite density.

2. The Nature of the Problem.

The problem of combating *Cephus cinctus*, Norton, in Canadian wheat fields led to the investigation of the parasitism of *Cephus pygmaeus*, Linn., in England (Salt, 1931), and thereafter to the annual shipment to Canada of overwintering *Cephus* larvae containing as high a percentage as possible of *Collyria calcitrator*, Grav., and other parasites. The preliminary work which is necessary each summer before the mass collecting is begun has resulted in the accumulation of some interesting data. Since the autumn of 1933 the *Cephus* collections have been made on farms round Cambridge, in particular from the Cherryhinton District, which lies to the east of the town. The procedure has been to examine samples of wheat from a number of fields in the area, a sample consisting of all the stalks in a patch of 1 square yard. The stalks are split lengthwise to find the *Cephus*, and every larva found is dissected. In this way the worker is able to form an estimate of the degree of infestation of the wheat by *Cephus*, and of the extent to which the sawflies are parasitized. The field finally chosen for the mass collection is the one which is expected to give the best yield of parasitized *Cephus*. In 1933, 1934 and 1935, the field work was undertaken by Mr. E. B. Basden and since then it has been in the charge of Mr. D. Berryman. Their careful records have supplied the data for this paper.

Mathematics may be applied to biological problems in more than one way. The simplest mathematical treatment is, of course, counting or measuring things or parts of things. Simple though these operations are, they involve difficulties. It is impossible to count all the things of a given kind that exist. In practice, the number must in some way be estimated from a *sample.* Furthermore, concrete things exhibit individual variation, so that the same parts may not be of exactly the same size in different specimens of the same species. The process of measurement itself involves the possibility of error ; successive measurements of the same thing may, for this reason alone, give different results. To decide in what degree samples of populations or sample measurements approach the real facts of nature, is the task of *statistics.*

The principles underlying statistical tests are derived, in the first instance, from pure mathematics. Thus, from the simple proposition that the probability that an event will happen is p and that it will not happen is q, the statistician derives the normal curve of error, of fundamental importance in statistical work. But though the equation for the curve is obtained by a perfectly logical process and may be considered to have a general application, yet an attempt to *use* the curve involves a passage from the mathematical to the real order, to which the mathematical equation may have to be specially adapted.

Thus, since a die has 6 sides, we might suppose that the chance of getting any number on it is the same and is one in six. Experiment has shown, however, that the six sides do not turn up with equal frequency, apparently because of the fact that each point is scooped out of the surface of the die so that there is, for example, a considerable difference between the surface with 1 point and the surface with 6.

The development of statistics is therefore not purely mathematical, but necessitates the consideration of the facts of nature, by which the fundamental hypotheses are progressively corrected.

The quantitative relations that result from the interaction of organisms with each other and with the physical environment are far more complex than those with which the statistician usually has to deal. Attempts have been made to investigate them by purely deductive methods, through the study of mathematical theories of populations. These are constructed on assumptions which appear to be plausible, but which simplify phenomena to excess. There is thus a far wider gap between theory and facts than existed even at the origin of statistical studies. The theory of populations has been elaborately developed ; and conclusions of a remarkable and interesting character have been extracted from it.

The present writer is, however, convinced that these mathematical developments, made in most cases with no more relation to the facts of nature than is provided by the artifice of attaching biological words to mathematical symbols, throw little light on the real course of events. The mathematical theory of populations should be developed in connection with facts, that is to say, in connection with numerical values actually obtained in nature ; and the task of the investigator should be, not simply the elaboration and development of *a priori* conceptions, but the construction of a mathematical hypothesis from which the observed values can be obtained. This hypothesis, though it may not be directly verifiable, should at least be reasonable, *i.e.*, not in direct contradiction to any known biological facts. Using it, one may attempt to account for the facts as revealed in the data, always bearing in mind that the explanation offered, though plausible, is not necessarily the true one.

For example, in the above mentioned case of analysis of superparasitism, the data had been obtained from a very large sample of *Cephus* larvae. This sample was considered to be sufficiently large to be representative of the whole population of the wheat field ; and so the aim of the work was to devise a hypothetical account of the *Collyria* adults' behaviour which, when made to operate in mathematical symbols, would most accurately reproduce the observed facts. After a number of theories (*e.g.*, that the parasite eggs are distributed at random among the hosts irrespective of superparasitism, that the *Collyria* females avoid superparasitism when the parasite's movements betray its presence in a host) had been tested, the conclusion was that it is reasonable to assume that *Collyria* females can distinguish between healthy and parasitized *Cephus*, but that the smaller the proportion of healthy hosts, the more likely is a parasitized host to be re-attacked. All that was claimed for the particular combination of hypotheses selected was that, in so far as they produced a parasite distribution similar to what was actually found in *Cephus*, they could be said to form a description of the reactions of *Collyria* females to their hosts.

The real reactions of a *Collyria*, or any other insect, can never be known directly, but we can describe exactly the reactions of a pseudo-insect, created in the imagination. We can make it behave in the way that a real insect appears to us to behave, and try to make it produce the same numerical results. When it does, the important point is that we do not claim to have discovered something about its real counterpart, but merely to have suggested a reasonable explanation of its behaviour. In what follows the aim has been to make clear at every stage the relation between the mathematical investigation and the biological theories. It should be borne in mind that the theories are offered tentatively and that they will always be open to reconstruction should they be found to be in disagreement with any newly observed facts.

3. Parasite Host and Host-plant Density Relations.

Because of the agricultural practice of the rotation of crops, wheat is not in general grown on the same ground in successive years, and so the *Cephus* population, having to move from the field in which it emerges to a new situation, will not necessarily be expected to make a uniform distribution of the progeny throughout the crop. There will be a likelihood of a heavier infestation in that part of the field first encountered in the course of migration. If, however, a sufficient number of samples have been taken in any one field it is possible, by examining the relative numbers of stems and larvae, to find out if, independent of the areal variation of the infestation, any relation exists between the density of the stalks and the numbers of *Cephus* and *Collyria*.

Table I shows the data for several fields. As already mentioned each sample consists of all the stalks from a patch a yard square. In this Table the samples are arranged in ascending order of the number of stalks. Two points must be noted regarding the numbers of parasites shown in the Table. Firstly, superparasitism of the host larva is common with *Collyria calcitrator*, although only one parasite survives ; the others, with the exception of certain hard mouth-parts, being entirely destroyed. To determine the actual number of eggs that have been laid in a host in a case of superparasitism requires a more careful dissection than is convenient for a worker who is engaged primarily in a field survey. The numbers given, therefore, really represent the numbers of hosts parasitized by *Collyria*, and it is in this sense that any further reference to numbers of parasites is to be interpreted, in the present paper. Secondly, a few of the *Cephus* larvae are unavoidably damaged when the stalks are split. Parasites were not recorded from the badly damaged hosts, again because of the practical inconvenience. While this small discrepancy should not affect the relative numbers of healthy and parasitized hosts in any sample, it does not allow comparisons to be made between the densities of the larvae in a series of samples. The necessary corrections have therefore been made to give what are estimated to be the true parasite densities of the samples. The data from Field A will suffice to illustrate the arithmetical method adopted. The other series were calculated in the same way :

In the twelve samples from Field A a total of 611 *Cephus* was found. Of these, 61 were damaged and were unfit for further examination. 550 *Cephus* were dissected, of which 270 were parasitized by *Collyria*, therefore of 611 *Cephus* we should expect $\frac{270\times611}{550}=300$ to be parasitized. The details of the 12 samples are :—

Total no. of hosts		No. of hosts dissected			No. of parasites found				Estimated no. of parasites
47	—	44	=	3	19	+	1	=	20
63	—	57	=	6	25	+	3	=	28
40	—	36	=	4	19	+	2	=	21
59	—	52	=	7	29	+	4	=	33
78	—	70	=	8	38	+	4	=	42
55	—	48	=	7	33	+	5	=	38
38	—	36	=	2	5	+	0	=	5
50	—	46	=	4	25	+	2	=	27
44	—	38	=	6	12	+	2	=	14
48	—	47	=	1	25	+	1	=	26
67	—	56	=	11	31	+	5	=	36
22	—	20	=	2	9	+	1	=	10
611	—	550	=	61	270	+	30	=	300

The additional number of parasites for each sample is very quickly obtained by inspecting the products $\frac{19\times3}{44}$, $\frac{25\times6}{57}$, etc., and writing the results as the nearest integer, 1, 3, etc.

The most obvious features of the data in Table I are the variability and the irregularity of the numbers of the hosts and parasites in relation to the increasing numbers of stalks.

In the construction of Table II, the samples for each field have been divided into four groups, and the average taken of the number of stalks, *Cephus* and *Collyria*, respectively in each group. Thus from Field A there were twelve samples, so that the numbers in the first line of Table II represent the averages of the first three samples of Table I A, the numbers in the second line represent the averages of the second three samples of Table I A, etc., while the numbers in the fifth line of Table II represent the averages of the first five samples of Table I B and so on. The advantage of this method of grouping the samples over that of averaging them in groups of some constant number, say three, is that it enables the conditions in the several fields to be more readily compared. Another alternative would have been to group the samples in a field, taking the averages of, for example, those with not more than 200 stalks, those with 201–250 stalks, etc., and indeed this method is commonly used in statistical analysis, but its unsuitability in the present case will be quite evident later.

From Table II it is plain that the grouping of the samples has not by any means sufficed to eliminate that apparent irregularity of the distribution of the hosts and parasites with respect to the varying densities of wheat stalks. A rather surprising feature is that although each of the fields except D and T might be said to show *on the whole* an increasing number of *Collyria* per square yard, with an increasing number of stalks, only four fields, A, B, G and L show a corresponding increase in the number of *Cephus*. The number of *Cephus* per 100 stalks increases in successive groups in one field only, L, decreases more or less in four fields, A, B, D and G, and is indeterminate in the other three. The number of *Collyria* per 100 stalks increases in successive groups in fields G and L, decreases in fields A, D and T, and is indeterminable in three fields. Finally, the proportion of *Collyria* to *Cephus* increases with increasing density of stalks in three fields, C, F and G, decreases in three fields, A, D and T, and varies irregularly in the remaining two. Thus if there is any real tendency for a relation to exist between the density of stalks in different parts of a field, and the numbers of *Collyria* and *Cephus*, its effect is overweighed by the other factors which influence the distribution of the insects. Even the mean stalk densities of the eight fields provide no clue as to why the various series should show increasing numbers in some cases and not in others. The best that can be done is to see if the averages of the results from all the fields together will suggest definite correlations. The method of calculation is again most easily explained by an example :—

Number of *Cephus* per square yard.

A	...	(40·0	50·7	50·3	62·7)	each	$\times\frac{3}{50\cdot9}$	=2·36	2·99	2·96	3·69
B	...	(11·6	18·4	19·6	27·6)	,,	$\times\frac{5}{19\cdot3}$	=3·00	4·77	5·08	7·15
C	...	(33·5	49·5	41·7	45·7)	,,	$\times\frac{4}{42\cdot4}$	=3·16	4·67	3·92	4·31
D	...	(17·0	29·7	21·3	21·0)	,,	$\times\frac{3}{22\cdot3}$	=2·29	4·00	2·87	2·83
F	...	(39·7	58·2	50·7	40·2)	,,	$\times\frac{4}{47\cdot3}$	=3·46	4·93	4·39	3·40
G	...	(58·0	61·0	68·5	65·5)	,,	$\times\frac{6}{63\cdot2}$	=1·84	1·93	2·17	2·07
L	...	(11·3	11·3	19·7	27·3)	,,	$\times\frac{3}{17\cdot4}$	=1·95	1·95	3·40	4·71
T	...	(27·5	21·0	35·0	27·5)	,,	$\times\frac{2}{27\cdot8}$	=1·98	1·51	2·52	1·98
				Total ...		...	·908	20·04	26·75	27·31	30·14
				Average ...		...		22·1	29·5	30·1	33·2

The data for each field are multiplied by two factors, one being the number of samples per group and the other the inverse of the mean number of *Cephus* per square yard for all the samples from that field. The reason is that the four groups of field B were derived from five samples each and so the data from them are more reliable than those from say field A, in the case of which the groups were derived from only three samples each. Field B thus carries more weight in the average than field A in the ratio 5 : 3. Conversely the average density of *Cephus* in the samples from field A was 50·9 per square yard, while in field B it was only 19·3 per square yard. Since the general rule for the distribution of the *Cephus* in relation to the density of the stalks should be, if it exists at all, independent of the degree of infestation, the field A data would not necessarily be more accurate than the field B data on account of the higher numbers of *Cephus* present. To prevent the average being unduly influenced by the greater density of *Cephus* in field A in comparison with that of field B, the set of data for each field is divided by its respective average number of *Cephus* per square yard.

The resulting averages for the six columns of Table II are as follows :—

Number of stalks per square yard ...	...	130	162	181	221
,, ,, *Cephus* per square yard	...	22·1	29·5	30·1	33·2
,, ,, *Collyria* per square yard	...	8·3	9·6	11·6	13·2
,, ,, *Cephus* per 100 stalks ...	...	17·0	18·2	16·6	15·0
,, ,, *Collyria* per 100 stalks ...	...	6·4	5·9	6·4	6·0
,, ,, *Collyria* per 10 *Cephus*	...	3·8	3·3	3·8	4·0

From the results it appears that in a wheat field the densities of *Cephus* and *Collyria* are in some way correlated with the variations in the density of the wheat stalks, being greater in the more dense areas of the field. The number of *Collyria* per 100 stalks is approximately constant, and shows no tendency to increase or decrease. It is therefore independent of the density of the stalks, and so we should

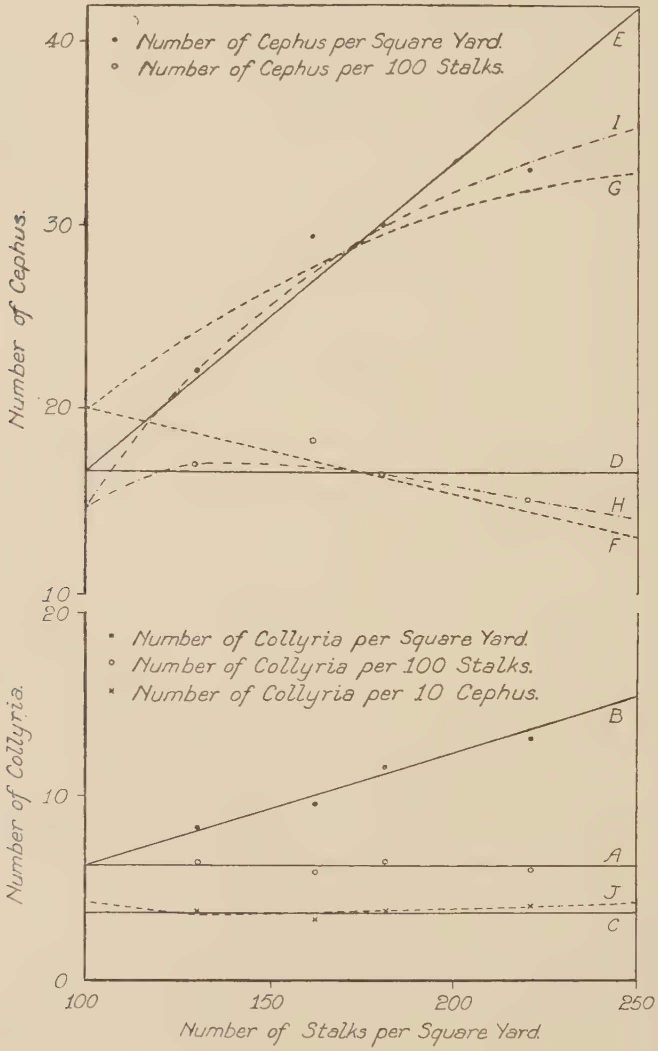

Fig. 1.

expect the number of *Collyria* per square yard to be directly proportional to the number of stalks per square yard. In fig. 1 the straight lines A and B show that this is a satisfactory representation of the data. The relation between the density of *Cephus* and the density of wheat stalks is not so easy to define. The four values for the number of *Cephus* per 100 stalks suggest neither a constant nor a tendency to vary in one definite direction. The values for the number of *Collyria* per 10 *Cephus* also show an irregular variation, but when they are represented graphically, as in fig. 1, it would seem that they might well be expressed by the constant 3·7, which is shown as the continuous line C. If, however, we take the number of *Collyria* per 100 stalks as a constant, 6·2, and the number of *Collyria* per 10 *Cephus* as a constant, it must follow that the number of *Cephus* per 100 stalks is a constant and that it has the value $\frac{6\cdot2\times10}{3\cdot7}=16\cdot8$. Further, if the number of *Cephus* per 100 stalks is constant at all densities of stalks, then the number of *Cephus* per square yard must be proportional to the number of stalks per square yard. The lines D and E in fig. 1 show that though this might be an adequate hypothesis, it does not appear to be one calculated to give the best illustration of the numerical data. Two possible alternatives to this hypothesis are also shown in the figure, where they are represented by the paired graphs, FG and HI. The slope of the straight line F indicates that the proportion of *Collyria* to *Cephus* decreases at a constant rate as the density of stalks increases. The corresponding line G for the number of *Cephus* per 100 stalks therefore curves over to the right. In H the proportion of *Cephus* to stalks rises to maximum and then diminishes as the density of stalks increases. The line I for the number of *Cephus* per square yard is also distinctly curved ; it is also, apparently, a better illustration of the data than are E and G. The significance of these different hypotheses will be discussed later.

We now come to a consideration of the numbers of *Collyria* in relation to those of *Cephus* only. In Table III the numbers of stalks in the samples have been ignored. The sets of samples from the various fields have been re-arranged in ascending order of the numbers of *Cephus* per square yard. They have then been averaged in 2's, 3's or 4's, as the case may be, to give the four groups for each field in exactly the same manner as has been described for Table II. From the new table it can be seen that in six out of the eight cases the number of *Collyria* per square yard definitely increases with the numbers of *Cephus* per square yard. In each of the two exceptions, fields F and G, there is an irregularity, but still, on the whole, the numbers increase. The numbers of *Collyria* per 10 *Cephus* are less determinate. Field A might be said to show an increasing proportion of *Collyria* to *Cephus* as the *Cephus* density rises, while Field B and possibly field C show decreasing proportions. Calculating the " weighted averages " for the three columns, as before, we have :—

Number of *Cephus* per square yard	...	17·3	24·8	31·3	41·3
,, ,, *Collyria* per square yard	...	7·5	9·5	10·2	15·7
,, ,, *Collyria* per 10 *Cephus*	...	4·3	3·8	3·3	3·8

The density of *Collyria* thus, on the whole, increases as the density of its host increases, while the nature of the variation of the ratio between *Collyria* and *Cephus* is still uncertain. The points along with three different pairs of graphs are shown in fig. 2. The continuous lines A and B show the effect of taking the average number of *Collyria* per 10 *Cephus* as a constant with the value 3·8 for all *Cephus* densities. The number of *Collyria* is thus directly proportional to the number of *Cephus* and B is a straight line passing through the second and third points. The line D is also straight but with a different slope. It was drawn in the figure as the result of only a rough estimate by eye of the general trend suggested by the points. The resulting line C for the ratio between the *Collyria* and the *Cephus* curves down very slightly from where C cuts the vertical axis and is quite a good fit for the points. The curved line F appears to be an excellent representation of the data, and its corresponding curve E is satisfactory too. The upward curving of F indicates the hypothesis that as the density of *Cephus* increases the relative number of *Collyria* increases too, according to a law defined by the shape of F.

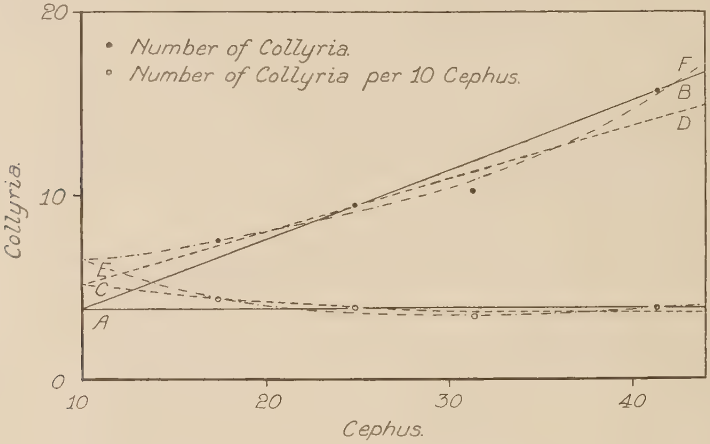

Fig. 2.

4. Analysis of the Numerical Data.

It has already been pointed out, and it cannot be too strongly emphasised, that the most striking feature of the data was their extreme variability. When a general law can be applied to account for the facts of nature, a certain amount of variation about the mean value designated by the law is always expected and is allowed for in statistical calculations. The difficulty in the present problem is that even grouping the samples has not sufficed to overcome the variability, *i.e.*, not so much the irregularities within the sets of samples from the several fields, as the unexpected differences which occur between the sets. One grave danger, however, has been avoided, and that because the present writer was not confronted with the problem until the facts had been carefully recorded time after time by workers whose object each year was to find the greatest number of *Collyria* larvae, *i.e.*, a good *Cephus* infestation with a high percentage of parasites, and who did not mind whether it happened to turn up in a good field of wheat or a bad one. The data given for each field represents the splitting and careful examination of some 2,000 stalks and on top of that the dissection of the larvae found, which altogether is not a trifling pastime, but a fairly large piece of hard work. Suppose then that the problem had been tackled on the basis of the information obtained from any *one* of the fields. If D had been the only field studied one might in all good faith have invented a theory of relations in which it would have been pointed out from Table II that while the *Cephus* tend to avoid ovipositing in the more sparse parts of the field, they have a preference for a certain range of stalk density rather less than the maximum found in this field. The *Collyria* too have a preference for this density of round about 220 stalks per square yard, but they do not avoid the thin places on the field. The attraction of the *Collyria* to this certain density of stalks has evidently not very much to do with the greater abundance of *Cephus* in such areas, since if it had, we should have expected a higher number of *Collyria* per 10 *Cephus* in them. And now suppose that, instead, the field G had been taken. The above theory cannot even be stretched to fit the facts here. The *Cephus* here seem to prefer a much higher density of stems for their greatest activity. The *Collyria*, in contrast to those of field D, avoid the poorer parts of the crop and are present in great numbers in the denser parts of the crop, reaching a maximum where the stems are most numerous. The extent of their increase far outweighs the possibility of its being due to the greater numbers of hosts present.

Each of those theories, if examined solely in connexion with the limited data on which it is based, is fairly plausible and could quite well be discussed in terms of certain of the general ideas of animal interaction.

It should be quite obvious, after what has just been said, that the analysis of the body of data, taken as a whole, must be undertaken with great caution and that the broad outline only of a theory will be more satisfactory than too much detail.

Returning now to fig. 2, we recall that it shows three pairs of graphs giving possible relations between the *Collyria* and the *Cephus*, when they are considered independently of the density of the wheat-stems. A is horizontal, which means that there is a constant number of *Collyria* per 10 *Cephus* at all densities of *Cephus* in a field ; so that the corresponding line B, representing the relation between the number of hosts and the number of parasites, is straight and passes through the points (3·8, 10) (7·6, 20), etc. It also passes through the origin (not shown), *i.e.* no matter how scarce the *Cephus* larvae are in any particular part of an infested wheat field, the corresponding proportion of *Collyria* larvae may be expected. Mathematically B did not seem to be a good enough fit for the four points. D is another straight line, apparently more suitable than B, and because it intersects B it cannot pass through the origin. The interpretation is that the number of *Collyria* is directly proportional to some "*part*" of the number of *Cephus*. D passes through the points (8, 20) and (5·1, 10). Therefore it goes through the points (2·2, 0) and (0,—7·6). In mathematical language this means that the number of *Collyria* is proportional to (the number +7·6) of *Cephus*, that there are 2·2 *Collyria* per square yard where there are 0 *Cephus*, and that there are 0 *Collyria* per square yard where there are —7·6 *Cephus* per square yard, all of which, biologically, is absurd. In the same way, the curve F, which was deliberately drawn as a good fit for the points, could be shown to given an even greater number of *Collyria* where the host *Cephus* is entirely absent. This means that we are left with the original simple hypothesis illustrated by the straight lines A and B, namely that as the density of *Cephus* larvae varies in a wheat field, the density of *Collyria* larvae is, on the average, directly proportional to that of the *Cephus*.

We might have said that the lines D and F represent theories which might be true biologically between some particular values, just as, for example, the equation of the catenary, taken between certain limits, is considered to be a convenient representation of the relationship between temperature and the rate of larval development in insects. But in the latter case, the limiting points external to which the shape of the curve is no longer true, correspond roughly to biological temperature limits, at which physical changes interfere with the metabolism. In the present problem no such definite natural limits suggest themselves, and it is better to avoid hypotheses in which they would have to be postulated and be assigned with arbitrary values. It may be objected that the straight line B, having passed downwards through the point (0, 0) enters the quadrant dealing with negative numbers of parasites in negative numbers of hosts ; but a moment's reflection will show that this does not have the unreal quality of positive numbers of parasites in negative numbers of hosts. If 10 oranges contain 20 pips each and we take away 2 oranges, we can write 10—2=8 for the oranges ; we must also write 200—40=160 for the pips, and the minus pips belong to the minus oranges.

There can be no doubt from fig. 1 that the relation between the numbers of *Collyria* and the numbers of stalks in different parts of a field is adequately expressed by the straight lines A and B. The number of *Collyria* per 100 stalks is constant at all densities of stalks, while the density of *Collyria* is directly proportional to the density of stalks. Since each point on the graph has been obtained as the result of smoothing out a great many irregularities, there can be no justification for attempting to find a closer mathematical fit.

In the case of *Cephus*, if we say that it is not sufficient to assume that the number of *Cephus* per 100 stalks is the same, however the density of stalks in a field varies, then the next theory to be examined is that the number of *Cephus* per 100 stalks decreases at some constant rate as the density of stalks increases. Illustrated in fig. 1 (F) is the case where the relation between the number of *Cephus* per 100 stalks and the density of stalks is expressed by the straight regression line $x+21{\cdot}4y=531$, which was calculated by the method described in Fisher (1928, p. 115). G is the corresponding curve for the relation between the density of *Cephus* and the density of stalks. Now we could draw an infinite number of pairs of lines like F and G and they would be such that as the slope of F diminishes and F approximates to D, G would swing round, and gradually straighten out to approximate to E. All the lines F are of the form $x=a-by$ (a and b positive) which means that at a density of x stalks per square yard, the number of *Cephus* per 100 stalks is $\frac{a-x}{b}$. Hence the density of *Cephus* per square yard is given by $\frac{a-x}{b}\cdot\frac{x}{100}$, so that the lines G are all of the form $y=\frac{ax}{100b}-\frac{x^2}{100b}$. The line $x=a-by$ cuts the x axis at $(a, 0)$ for all values of a and b. Biologically this would mean that at certain high density of stalks, the number of *Cephus* per 100 stalks is 0, and that at densities higher than this it is negative, which is impossible. However, for the particular F illustrated, this theoretical critical density is 531 stalks per square yard, a number very much greater than any which was actually found in the samples (see Table I). The density of the wheat stalks per square yard varies considerably, not only within a given field, but, on the average, between one field and another. Nevertheless, no matter how lavishly the grain were sown, or how rich the soil, there would be a natural upper limit to the number of stems growing per square yard ; but long before this limit was reached the overcrowding of the plants would have caused such a reduction in size and vigour of the stalks, that such parts of the crop would be unacceptable to the ovipositing *Cephus* for practical reasons. The curve G, $y=\frac{ax}{100b}-\frac{x^2}{100b}$ passes through the origin and cuts the x axis again at (a, 0). It is a parabola and passes through a maximum at the point $\left(\frac{a}{2}, \frac{a^2}{400b}\right)$. In other words, the density of *Cephus* is zero when the density of stalks is zero and again, as we should expect, where the number of *Cephus* per 100 stalks has diminished to zero, while the *Cephus* are " negative " where the stalks are " negative " and when they are more dense than a per square yard. The maximum number of *Cephus* occurs where the density of stalks is one-half of the critical density and is equal to $\frac{a^2}{400b}$. Although F in fig. 1 was the calculated straight regression line, it can be seen that this particular pair of lines F and G do not together make a good fit for the points. A more satisfactory representation is obtained if F is through or just above the 3rd and 4th points, in which case G passes through (or just above) the corresponding points. The lines are omitted from the figure to avoid confusion. Because all the straight lines of the F series cut the x axis sooner or later, this hypothesis would have to be rejected on account of the biological absurdity included, were it not for the operation of the limiting factor, the stalk density. According to the figure and the calculations above, the number of *Cephus* per 100 stalks diminishes to zero at a density of stalks not less than 531 per square yard and according to the data the maximum number of stalks per square yard is, in practice, not more than about 360. In this respect the theory *could* be true for the extent to which it is *likely* to be true.

The straight line E for the density of *Cephus* in relation to the density of stalks was derived from the assumption that the number of *Cephus* per 100 stalks was a constant and could be represented by the horizontal straight line D. A simple alternative to E was the straight line for the regression of the stalk density in the *Cephus* density. It has the equation $x-6{\cdot}3y+7{\cdot}3=0$ so that it passes through the points (0, 1·16) and (−7·3, 0), *i.e.*, the number of *Cephus* per square yard is 1·16 when the density of wheat stalks is zero, and when the density of *Cephus* is zero there are −7·3 stalks per square yard—a biological absurdity which calls for the rejection of the regression line as a possible representation of the facts. The same fallacy would occur for any straight line, other than E, which the eye might suggest as a possible fit for the points in question.

If the proportion of *Cephus* to stalks is to be represented by a curve instead of by a straight line, we could start off by drawing a simple curve to fit the points as nearly as possible, arranging it to have a maximum in the desired place. A parabola or a hyperbola might meet the case. Alternatively, if a curve is drawn to fit the *Cephus* density points, the curve derived from it must automatically fit the *Cephus* ratio points. The lines H and I in fig. 1 are an example of the latter method. The curve I *happens* to be of the type $y=a\left(1-e^{-b(x-c)}\right)$. This class of curve is too well known in biomathematical studies to need any explanation here. But since the equation has become associated with the idea of randomness (*e.g.*, random distribution of parasite eggs among hosts, random searching of animals) it must be emphasised that it was the mathematical properties of the equation and not the biological concepts related to it which prompted its use in the present problem. I has the equation $y=40\left(1-e^{-\frac{2}{175}(x-60)}\right)$ it cuts the x axis at the point (60, 0) and has the line $y=40$ for an asymptote. The relation of H to I is such that for H, $y=\frac{100}{x}\cdot40\left(1-e^{-\frac{2}{175}(x-60)}\right)$ giving a curve which is asymptotic to the x axis and passes through a maximum at the point (145, 17·2). In terms of *Cephus* and the wheat stalks this amounts to saying that oviposition does not occur in parts of the field where the number of stalks per square yard is less than 60; that the number of *Cephus* per 100 stalks has its greatest value where the density of stalks is 145 per square yard, and that as the density of stalks increases this ratio falls, at a diminishing rate, to zero; finally, that where the density of stalks increases, so does the density of *Cephus* increase, but at a diminishing rate, so that it tends to a limiting value. The curves H and I are seen to fit the points quite well, but the writer can offer no explanation as to why the numbers of stalks and of *Cephus* larvae should be related to one another by an exponential function. The type of function came to mind because it was a familiar one, and it was known from experience that it would produce the necessary bending for I and the maximum for H. It was not used for any other reason, nor does the writer propose to invent any theory to account for its apparent success.

The straight line C, $y=3{\cdot}7$, in fig. 1 looked as if it were a good fit for the points showing the number of *Collyria* per 10 *Cephus* at different stalk densities, but since the hypothesis that the density of *Cephus* is proportional to the density of stalks has been improved on mathematically, if not biologically, we must evidently give a more exact picture than C, which means that the proportion of *Collyria* to *Cephus* tends to be constant at all parts of a field. If we accept I for the relation between the density of *Cephus* and the density of stalks, then J is the corresponding line for that between the number of *Collyria* per 10 *Cephus* and the density of stalks. J has the imposing equation $y=\frac{6{\cdot}2x}{400\left(1-e^{-\frac{2}{175}(x-60)}\right)}$ which is very simply derived from the equations of A and H. This equation, like that for H and I, has no obvious biological explanation and it need not be used in the arithmetical calculations for the points of the line. If, on the other hand, we take one of the lines from the series F to represent the relation between the density of *Cephus* and the density of stalks, a much simpler formulation exists for this *Collyria*-stalk density relation. The equation for the particular F shown in fig. 1 is $y=\frac{531-x}{21\cdot 4}$ and so the corresponding *Collyria* graph is $y=\frac{6\cdot 2\times 214}{531-x}$. This curve is a very flat hyperbola and to avoid confusion it has been omitted from the figure. From the equation it can be seen that as x increases up to 531, y continues to increase. In other words, as the density of stalks increases the ratio of parasites to hosts increases and this ratio is infinitely great where the density of stalks is 531 per square yard, because at that density the *Cephus* is entirely absent! This is a theory which might be true within the actual limits of the field conditions.

The final result of the analysis is that while more than one *possible* theory has come to light, there is not one in which the mathematical foundation can be identified obviously and in its entirety with a biological description of the case.

5. Theories of Insect Behaviour.

The arguments of the foregoing section may be summarised briefly as follows: Considered independently of the wheat stalks, the density of the *Collyria* parasites in the different parts of a field has been found to be on the whole proportional to the density of the *Cephus*. This is only roughly true, but it is not untrue in the sense that there is some other less simple law which would always describe the relation more accurately. In the same way, the density of *Collyria* tends within a field to be proportional to the density of stalks. The density of *Cephus* in a field is also, on the whole, greater where the density of stalks is greater, but the rate of increase is not constant and is such that the ratio between the number of *Cephus* and the number of wheat stalks must either decrease continuously with the increasing density of stalks, or decrease after having passed through a maximum. These findings will now be considered in connection with the problem of how parasites search for their hosts.

Nicholson (1933) said " Examination of the problem of searching shows that it is fundamentally very simple, provided the searching within a population is random. Before further investigation, therefore, we must find if it may safely be claimed that the searching within animal populations is actually random.

" It is important to realise that we are not concerned with the searching of individuals, but with that of whole populations. Many individual animals follow a definite plan when searching. For example, a fox follows the scent of a rabbit, and a bee systematically moves from flower to flower without returning on its course. However, there is nothing to prevent an area that has been searched by an individual from again being searched systematically by another, or even the same, individual. If individuals, or groups of individuals, search independently of one another, the searching within the *population* is unorganised, and therefore random. Systematic searching by individuals improves the efficiency of the individuals, but otherwise the character of the searching within a population remains unaltered. Therefore, when investigating the problem of competition, we may safely assume that the searching is random." This complete generalisation of the problem suggests that apparently Nicholson considers that he has circumvented the necessity of examining the behaviour of different kinds of animals in relation to their various instincts. Referring to his own observations on *Orgyia leucostigma*, Smith & Abbott, Howard (1897) said " The tussock-moth caterpillar is itself a slow traveller. Its primary parasites naturally congregate at the points of greatest caterpillar abundance. At points where the caterpillars are scarcer they are thus less exposed to the attacks of their parasitic enemies, and it results that there may actually be an increase of the species at one point simultaneously with a decrease at another." If one were to formulate a general law from the above observed fact, it would be quite reasonable to postulate that in the case of entomophagous parasites which must obviously possess the necessary instincts to link them to the specific hosts they require, the parasites will tend to congregate in greater numbers in localities where the host is more abundant. This does not seem to be in agreement with the theory of random searching quoted above, nor with Nicholson's development of it in the same paper ; but if he would claim that it is, then his failure to make himself clear must in some measure be due to his unfortunate choice of phrases. For how can it be said that searching within a population is unorganised if there is a common focus of attraction towards which all the individual efforts are directed ? Such searching would certainly be unorganised when contrasted with that which might be accomplished by a search-party of soldiers acting under detailed orders, but it is surely highly organised in comparison with the theoretical random searching from which Nicholson derived the " competition curve."

Different facts have been recorded for certain parasites which are less specific in their choice of hosts : According to Picard & Rabaud (1914) : " Il apparaît que, dans certains cas tout au moins, l'attirance exercée par un végétal donné est d'une plus grande importance que l'Insecte dont se nourrira la larve, et il en doît être ainsi pour le *Bracon scutellaris*, Wesm. qui se développe indifféremment aux dépens de *Grapholita strobilella*, des *Hylesinus*, etc., c'est-à-dire des insectes des Conifères, et pour le *B. colpophorus*, Wesm. qui attaque les Charançons des Légumineuses, que ce soient des *Apion* ou des *Laria*. Il nous a paru que le *Bracon variator*, Nees, était incité à pondre, non par l'approche d'un Insecte déterminé mais par celle des capitules des Composées, et entre autres des Carduacées." This passage is interpreted by the present writer to mean that hosts suitable for *B. variator* are not found by this insect unless they are in a particular type of environment.

Nicholson's theory could be true for cases such as these, once the parasites have arrived *within the environment* that attracts them. But in nature, animals (including some insects) very often have to travel considerable distances to obtain their requirements, and their method of doing so is the reverse of random, it is the directed response to an impelling instinct. *Collyria calcitrator* is specific in its choice of host, yet it too behaves in the manner described by Picard & Rabaud, being, as we shall see, apparently attracted primarily by a particular environment associated with the host, rather than by the hosts themselves.

In 1935 the preliminary examination was extended to oats and barley. An infestation of *Cephus* quite comparable to the average in the wheat fields was found in the samples from the barley field and from one of the fields of oats. Only one *Cephus* larva was found in 900 stalks from a second oat field, and none at all in 1,100 from a third. Now although there is always considerable variation in the degree of infestation of the wheat fields of this particular area at Cherryhinton, the *Cephus* are never entirely absent from the wheat. The contrast between the different fields of oats is therefore surprising. One possible explanation is that *Cephus* is attracted chiefly to the wheat, the attack of the other crops being merely a sort of overflow from the wheat fields. The percentage infestations of the stems do not immediately suggest that there has ever been a shortage of stems for the ovipositing females. It must, however, be remembered that egg-laying takes place while the crop is still in a phase of active growth and that a considerable proportion of the stalks may either be rejected by the *Cephus* as too thin, or be overlooked altogether because they are too short at the time.

The field of barley already mentioned had one corner adjacent to a heavily infested wheat-field. A study of the samples in relation to a plan of the fields shows that the hypothesis of overflow is not impossible. The barley field was L-shaped and the *Cephus* infested oat-field was situated between the arms of the L. The infestation was, on the whole, less than that of the barley, 35 per square yard, as compared with 59. On the other hand, lying alongside this self-same wheat-field was the field of oats from which *Cephus* was for all practical purposes absent. If the hypothesis is to be true, there must have been something particularly unsuitable about this crop, for example, that it was sown very late.

An alternative theory is that while *Cephus* has the instinct to find wheat and will migrate from field to field after it in successive years, grain crops other than wheat will be attacked only if they follow immediately after wheat in a field, *i.e.*, they do not actually attract, but they will serve the purpose. According to the laboratory records, the groups of fields under discussion were not examined in the previous year, 1934, so we do not know what was grown there. It should be noted that the land in this district is sown with grain more frequently than is the case with the usual rotation of crops.

Of the *Cephus* from the barley, a large number was dissected. Out of 367 larvae, only 2 were parasitized with *Collyria*, yet in the adjacent wheat-field the parasitism by *Collyria* was 23 per cent. The *Cephus* from the oats were unfortunately not dissected. The attack of *Cephus* by *Collyria* is thus an instinctive action which apparently must follow as a sequel to the attraction of the adult *Collyria* to wheat. If the first of the two attempts to explain the presence of *Cephus* in barley and oats is correct, then we should say that in the present case the *Collyria* adults might eventually have followed the *Cephus* into the other crops if the percentage parasitism in the wheat had risen so that hosts became relatively scarce. But if the second hypothesis is the correct one, there has obviously been no adaptation in *Collyria* corresponding to *Cephus*' acceptance of host plants other than wheat, and the emerging *Collyria* females must have moved away in search of wheat without being aware that their hosts were in the immediate vicinity. This point could probably be cleared up after some further field observations and an enquiry into the history of the fields.

At this point it is interesting to note the parallel case of the western grass-stem sawfly, *Cephus cinctus*, Norton. In Canada this insect is one of the major pests of wheat, which it began to infest about the beginning of the present century. While the sawfly confined its attack to wild grasses, its numbers were believed to have been controlled by the limited number of grass-stems big enough to house the larvae as it grows, and by the action of parasites (Criddle, 1922). Its discovery of the new domain of wheat provided this sawfly with an almost inexhaustible supply of stems suitable for attack. The parasites of *C. cinctus* in its natural habitat did not accompany it successfully into the wheat fields. Ainslie (1920) points out that though in some districts of North Dakota, *Pleurotropis utahensis*, Cwfd., attacks the sawfly freely in Bromus and Timothy grass, and may kill more than 50 per cent. of the larvae, very few parasites were found in wheat stems, however numerous the hosts might be. He too suggested that the parasites were unaware of the presence of their hosts in the wheat-fields, but was hopeful that in time their habits would become adjusted to the altered circumstances. Another opinion put forward is that the ovipositors of the grass parasites are too short to reach the *Cephus* through the thicker wheat stems (Thompson, 1930).

A certain attraction, possibly odour, leads *Collyria* females to wheat in search of *C. pygmaeus* larvae. But what is their method of searching once they have reached the wheat ? Have they any instinct which directs them to the infested stalks ? Probably not, for the females have been observed to fly from stem to stem, examining each in turn by running down it to within 6 inches or so of the ground, and then up again, tapping with the antennae all the while. More often than not no attempt at oviposition is made during this performance. Again, if these hosts could be located from a distance by the parasites, we should expect that the *Cephus* in barley would be attacked more often than was actually the case. The density of the parasite larvae was found to be proportional to the density of *Cephus* larvae. This could support Nicholson's theory of random searching. According to this theory the whole area is searched at random by the parasites, irrespective of the variations in the density of hosts in different regions of it. Consequently, when all the parasites have ended their searching, a certain fraction of the area has been covered, and that same fraction of the hosts has been parasitized in every part of the area. The facts referred to do not, however, constitute a proof of the theory. We say from the data, that in any given part of the field the number of hosts attacked is proportional to the number of hosts, *i.e.*, the number of *Collyria* offspring is proportional to the number of hosts. But the number of *Collyria offspring* is equal to the number of adult females in that part of the field, multiplied by *their* average rate of reproduction. Hence to obtain parasite larval numbers proportional to host numbers, we may have :—(1) adult parasite density constant and reproductive rate proportional to the number of contacts with hosts, *i.e.* to host density ; (2) adult parasite density proportional to host density, and reproductive rate constant ; or (3) (an intermediate condition) both increasing with, but not in proportion to, host density. There is no way of telling which of the three is true. It may depend on whether the population of adult *Collyria* is large or small in proportion to the population of host larvae. If large, then the first case, which represents Nicholson's random searching theory, seems the more likely. If small then the second case, which is in a sense a parallel with Howard's observations on the tussock moth parasites, is the better hypothesis.

It was suggested above that at the season when the female *Cephus* are ovipositing, they may find that only a fraction of the stems are sufficiently far advanced for their acceptance. This means that a final infestation of say 25 per cent. of the stalks would represent a very much higher percentage infestation of the material available at the time of oviposition. The theory would also help to account for the way in which the density of *Cephus* larvae varies with the density of stalks. Assuming that the distribution of the adult *Cephus* about the field is independent of the variation in stalk density, then the females in the denser parts would be more likely than those in the less dense parts to be able to find suitable situations for *all* their eggs. This would justify the use of a curve of the type I in fig. 1 to represent the relation between the density of *Cephus* larvae and the density of stalks. It will be remembered that the feature of this curve is that the density of *Cephus* increases continuously with the density of stalks, but tends asymptotically to an upper limit. The asymptote is now explained, for with any given average density of adult females per square yard, it represents the maximum number of their eggs per square yard. The data in Table II for fields B and L are in agreement with the idea. Those two fields have particularly low densities of stalks, and there is no sign in them of the asymptotic trend of the *Cephus* density curve, *i.e.* the *Cephus* in those fields had had little opportunity of exhausting their egg supplies.

Taking the average of the eight fields, the density of *Collyria* larvae was found to be in direct proportion to the density of wheat-stalks. Now it is obvious that if there were one hundred per cent. parasitism, the curve for the relation between the densities of *Collyria* and stalks would have to be exactly the same as the corresponding curve for *Cephus* and stalks (superparasitism being ignored). Therefore we should expect that in fields with very high average percentages of parasitism there would be some sign of the *Collyria*-stalk relation behaving like that between the densities of *Cephus* and stalks, namely the density of *Collyria* increases with increasing stalk density, but at a diminishing rate. From this it would follow that with very low average percentages of parasitism there would need to be a compensating effect so that as the stalk density increases the proportion of *Collyria* to stalks increases too. This last deduction is supported by the data—see the final columns concerning fields F and G in Table II—and if these deductions are true, the inference must be that the *Collyria* females have the tendency, not to distribute themselves more or less uniformly throughout a wheat field, but to congregate in the parts of the field where the stalks are more numerous. Hence if the adult *Collyria* population has on the whole a very low density, the competition for host larvae will not be severe even where the parasites are more numerous, so that none of the adults will be debarred from laying their eggs because of a scarcity of hosts. Therefore a greater proportion of hosts will be attacked where the stalks are more numerous. But if the adult *Collyria* population has a relatively high density, their egg-laying activities become limited by the numbers of the hosts, and the competition will be very much more severe in the denser parts of the field where not only are the female parasites more numerous, but also the density of host larvae is no longer increasing in proportion to the density of stalks.

The above hypothesis of the distribution of *Collyria* may be interpreted in two ways. Because the *Collyria* do not attack *Cephus* in barley, it is known that they must be attracted to wheat before they can locate their hosts. Once they have reached the wheat field, a slight preference for the more dense areas of the field might be due simply to the stronger attraction of the greater bulk of wheat. On the other hand, it might be due to the attraction of the greater numbers of hosts. A similar point, it will be remembered, was left undecided in the discussion of the ratios between the host and parasite densities independent of the stalk densities, a ratio which was constant at all host densities. If the attraction of the parasites to the denser parts of the field were due to the attraction of the greater numbers of hosts, then it seems, in the light of all the evidence, that when the parasite and host densities were correlated independently of the numbers of stalks, the ratio between them should have been found to increase where the host density increased. So the alternative theory remains that in any wheat field the *Collyria* females tend to be more numerous in the denser areas of the field than in the sparsely sown areas, because the greater quantity of wheat exercises a stronger attraction. The *Collyria* have no knowledge of the existence of a host in a particular stem until that stem is investigated. Consequently they must move from stem to stem until they find the desired host. This is confirmed by direct observation of their behaviour under natural conditions.

In so far as the accepted hypotheses are true, the behaviour of *Collyria* within the specific environment of the wheat field has been shown to be a fairly good example of " random searching " in the sense of Nicholson. An obvious discrepancy arises out of the assumption that there will be more females where the stalks are denser, for it is thus no longer true either that every small unit of area is likely to receive the same number of visits from females, or that every stalk is equally likely to be examined. To have true random searching in a field, according to the mathematical meaning of random, one or other of these conditions would have to be fulfilled, the first if the searching were random with respect to area, the second if it were random with respect to stalks. The theory of Nicholson implies that animals search *areas* at random.

6. The Seasonal Variation of Populations.

In conclusion attention is drawn to an important angle of the problem, namely, the way in which a *Cephus* population varies from field to field and from year to year in the same area.

Table IV consists of a summary of all the available data for the wheat fields of the Cherryhinton district, the fields in each year being arranged in ascending order of severity of the *Cephus* infestations. The figure for each field represent the averages of various numbers of square yard samples. In some instances the number of samples was as low as three, so it is to be understood that no great degree of accuracy is claimed. The collections were all made within a total area of not more than one square mile, an area of which at least two-thirds is sown with wheat annually. In the comparison of the infestations of different fields in the same year, the great range in the average numbers of *Cephus* per square yard should be noted. With the exception of the two very thin fields in 1937 which have also relatively low numbers of *Cephus*, there does not appear to be any correlation between the density of the *Cephus* infestations and the density of the crops, such as has been shown to occur *within* the fields. There is also a great variation in the density of *Collyria*, but the percentage of parasitism is independent of the density of the hosts.

If one were to try to find an explanation of the figures in Table IV in terms of Nicholson's theory of the Balance of Animal Populations, the problem would be extremely complex. In addition to the parasitism by *Collyria*, *Cephus* is attacked in less degree by a number of other parasites. There is also the phenomenon of its almost complete immunity from *Collyria* when it infests barley, while the continual changing of the environment due to the way in which the crops are varied in the fields adds to the difficulties. Most of those points are dealt with in the mathematical arguments of Nicholson & Bailey (1935), but even if the data were increased a hundredfold one would not feel justified in attempting to fit the numbers representing the facts to the equations of their mathematical deductions. In his earlier paper Nicholson (1933) says " The more important conclusions that have been obtained by a study of the problem of the competition that exists between animals when searching are given in . . . . . . this paper. The conclusions inevitably follow from the formulation of the problem already given, but for their rigorous proof much use needs to be made of mathematics, and it is thought desirable to postpone this to subsequent publications. However, when possible, brief general arguments are given to show that the conclusions are entirely reasonable." In the summary of the same paper he says : " Competition always *tends* to cause animals to reach and to maintain their steady densities. Factors, such as climate and most kinds of animal behaviour, whose action is influenced by the densities of animals, cannot themselves determine population densities, but they may have an important influence on the values at which competition maintains these densities " and further " . . . . in a constant environment the densities are caused eventually to reach, and to remain at, their steady values." " However, the environment does not remain constant, and it is found that periodic environmental changes, such as those of the seasons, tend to impress their period upon interspecific oscillation. Consequently, the oscillation that is produced by the interaction of animals should generally be found to correspond in time with seasonal and other periodic environmental changes, but its violence is greater than that of the oscillation which these environmental changes could themselves produce."

Nobody would think of denying that the properties of the environment affect the numbers of animals living there. But it is not so certain that Nicholson has justified his statement that the oscillations of the population densities that are produced purely by the interactions of the animals themselves are greater than those produced by seasonal and environmental changes, for how, in actual fact, could one ever dissociate the effects of the two types of phenomena ? The weather plays an individual part in every season, and however accurately we may assess its effects on mortality and reproduction for any particular period in the past, we can never foretell its rôle for the future, nor may we justifiably assign to the unknown a value based on an average of previous events. For example, a season in which the infestation by *Cephus* was very high might be followed by particularly adverse winter conditions which might possibly wipe out the entire larval population in one area. In such a case, the tendency for the restoration of the normal host density would have to be due, not to the compensating effect of an increased *Collyria* population, but to the infiltration of a new stock of *Cephus* from an area less severely influenced by the weather.

The application of mathematics enabled Nicholson & Bailey (1935) to make a long series of deductions concerning the delicate interplay of *bersmun* of animals under certain conditions. The theory is a beautiful one from the standpoint of abstract reasoning, but we should not expect to find in nature the counterparts of its conclusions. Nicholson (1933), in the general argument, stated a number of conclusions concerning the effects of factors which vary the environment, but these are not, as he claims, deductions which inevitably follow from the initial formulation of the problem. They cannot be real deductions unless laws stating *how* the environment is altered are included in the hypotheses and this does not seem possible, at least not yet. Nicholson's (1933) final conclusion is : " Competition regulates the densities of animals in erratically and progressively changing environments just as it does in undisturbed environments " ; but we may conclude here by pointing out that since nature does not offer us any undisturbed environments in which to study exactly how competition regulates the densities of animals, we are not likely to arrive at an accurate solution of the problem in the erratically and progressively changing environments which do occur.

7. Summary.

For the past six years samples of wheat from the various wheat fields at Cherryhinton near Cambridge have been collected. These samples were examined for an estimate of the incidence of *Cephus pygmaeus*, Linn., and its parasites, chiefly *Collyria calcitrator*, Grav. The present investigation is an analysis of sets of samples from different fields.

The data in their original form consisted of the numbers of stalks in square yard samples, the numbers of *Cephus* larvae in the stalks, and the approximate numbers of *Collyria* larvae in the *Cephus*. Cases of superparasitism, which is known to be common with *Collyria*, had not been recorded, but by making allowances for the material damaged in collection it was possible to make an estimate of the number of *Cephus* parasitized by *Collyria* in each sample.

The samples in each field were arranged in ascending order of density of the stalks and were then averaged so as to form four groups. They were also arranged in ascending order of the density of *Cephus* and a similar process carried out. Within the individual field there appeared to be some correlation between the densities of the stalks and the densities of *Cephus*, and again between the densities of *Cephus* and of *Collyria*, but the process of averaging did not sufficiently smooth out the irregularities to enable laws of correlation to be formulated.

The next step was the drastic one of taking an average for all the fields together, the data for each field being weighted according to the number of samples represented. This enabled the following conclusions to be reached : Considered independently of the wheat-stalks, the density of the *Collyria* larvae in the different parts of a field is on the whole in direct proportion to the density of the *Cephus*. In the same way, the density of *Collyria* tends within a field to be proportional to the density of stalks. The density of *Cephus* is also greater where the density of stalks is greater, but the rate of increase in *Cephus* density falls off with the increase of stalk density. Mathematical curves which appear to represent the latter relation are given. These generalisations are only roughly true and the data from the different fields deviate from them. The suggestion is that they represent the underlying state which might exist but for factors which vary from place to place, *e.g.*, food-plants, and from time to time, *e.g.*, winds.

The *Cephus* will attack barley, but so far the parasitism by *Collyria* of *Cephus* in barley has been found to be negligible. This and other observations suggest that the attraction to which *Collyria* reacts is not the host larvae themselves but their habitual environment, wheat. It follows then that the actions of female *Collyria* within a wheat field may be taken as a fairly accurate example of searching at random for hosts.

Data are given showing the way in which the population of the host and its principal parasite vary from year to year. The conclusion is that the diversity of the biological and physical factors, and particularly the uncertainty of the latter, preclude any satisfactory analysis of the numerical inter-relations such as would be necessary to prove or disprove a mathematical theory of animal interaction.

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TABLE I.

A. Netherhall Farm, 1933			B. Netherhall Farm, 1934			C. Rectory Farm, 1934		
Stalks	*Cephus*	*Collyria*	Stalks	*Cephus*	*Collyria*	Stalks	*Cephus*	*Collyria*
110	22	10	54	11	4	177	40	20
190	48	26	57	11	6	193	29	15
197	50	27	60	5	0	203	27	12
232	55	38	61	15	7	210	38	9
234	38	5	62	16	9	216	44	20
244	59	33	80	19	3	221	45	21
248	40	21	82	15	2	230	63	20
256	44	14	82	26	6	233	46	21
258	67	36	91	16	7	236	46	18
268	78	42	95	16	2	239	46	17
313	63	28	104	13	7	247	37	23
356	47	20	104	13	8	249	38	18
			105	34	7	263	37	24
			105	17	3	268	54	27
			113	21	9	270	46	21
			118	18	1			
			138	26	13			
			159	28	4			
			172	40	16			
			180	26	14			

D. Rectory Farm, 1934			F. Rectory Farm, 1935			G. Rectory Farm, 1935		
Stalks	*Cephus*	*Collyria*	Stalks	*Cephus*	*Collyria*	Stalks	*Cephus*	*Collyria*
167	8	4	151	52	3	158	50	8
191	9	8	184	39	6	207	66	10
200	34	30	185	48	9	224	51	16
216	17	12	191	20	2	242	71	14
221	44	36	192	79	14	247	73	22
228	28	16	203	49	4	266	64	16
239	19	16	209	58	*	279	57	23
240	21	15	210	47	6	303	74	23
245	24	16	212	30	9			
253	29	20	216	60	17			
263	22	13	224	63	11			
263	12	10	225	50	*			
			240	29	8			
			241	59	4			
			271	32	11			
			308	43	14			

L. Netherhall Farm, 1937			T. Netherhall Farm, 1938		
Stalks	*Cephus*	*Collyria*	Stalks	*Cephus*	*Collyria*
90	17	7	138	20	14
112	7	4	172	35	20
118	10	5	199	12	6
125	16	5	205	30	14
126	7	3	215	38	10
131	13	5	235	22	10
131	9	4	235	42	17
143	26	11	271	23	8
148	22	6			
153	24	13			
197	24	6			
206	34	14			

* The *Cephus* in these samples were not dissected.

TABLE II.

Field	No. of stalks	No. of *Cephus*	No. of *Collyria*	No. of *Cephus* per 100 stalks	No. of *Collyria* per 100 stalks	No. of *Collyria* per 10 *Cephus*
A	166	40	21·0	24·1	12·7	5·2
	237	50·7	25·3	21·4	10·7	5·0
	254	50·3	23·7	19·8	9·3	4·7
	312	62·7	30·0	20·1	9·6	4·8
B	59	11·6	5·2	19·7	8·8	4·5
	86	18·4	4·0	21·4	4·7	2·2
	106	19·6	6·8	18·5	6·4	3·5
	153	27·6	9·6	18·0	6·3	3·5
C	196	33·5	14·0	17·1	7·2	4·2
	225	49·5	20·5	22·0	9·1	4·1
	243	41·7	19·0	17·2	7·8	4·6
	267	45·7	24·0	17·1	9·0	5·3
D	186	17·0	14·0	9·1	7·5	8·2
	222	29·7	21·3	13·4	9·6	7·2
	241	21·3	15·7	8·8	6·5	7·3
	260	21·0	14·3	8·1	5·5	6·8
F	178	39·7	5·0	22·2	2·8	1·3
	203	58·2	8·0	28·6	3·9	1·4
	219	50·7	12·3	23·1	5·6	2·4
	265	40·2	9·2	15·2	3·5	2·3
G	182	58·0	9·0	31·8	4·9	1·6
	233	61·0	15·0	26·1	6·4	2·5
	256	68·5	19·0	26·7	7·4	2·7
	291	65·5	23·0	22·5	7·9	3·5
L	107	11·3	5·3	10·6	5·0	4·7
	127	11·3	4·2	8·9	3·3	3·8
	141	19·7	7·2	14·0	5·1	3·6
	185	27·3	11·0	14·8	5·9	4·0
T	165	27·5	17·0	14·5	11·0	6·2
	202	21·0	10·0	10·4	5·0	4·8
	225	35·0	15·3	15·6	6·8	4·4
	253	27·5	10·7	10·9	4·3	3·9

TABLE III.

Field	No. of *Cephus* per sq. yard	No. of *Collyria* per sq. yard	No. of *Collyria* per 10 *Cephus*
A	33·3	12·0	3·6
	46·3	20·0	4·3
	54·7	32·7	6·0
	69·3	35·3	5·1
B	10·6	5·0	4·7
	15·6	5·4	3·5
	20·2	6·0	3·0
	30·8	9·2	3·0
C	32·5	18·8	5·8
	40·0	16·8	4·2
	45·8	19·7	4·3
	54·3	22·1	4·1
D	9·7	7·3	7·6
	19·0	14·3	7·5
	24·7	15·0	6·1
	35·7	28·7	8·0
F	27·8	8·0	2·9
	43·0	8·8	2·0
	49·7	5·3	1·1
	64·8	11·5	1·8
G	50·5	11·5	2·8
	60·5	19·5	3·4
	68·5	12·0	1·8
	73·5	22·5	3·1
L	7·7	3·7	4·8
	13·0	5·0	3·8
	21·0	7·5	3·6
	28·0	11·5	4·1
T	16·0	8·0	5·0
	22·5	11·5	5·1
	32·5	14·0	4·3
	40·0	19·0	4·8

TABLE IV.

Year	Averages for the Fields				Averages for the Area		
	Stalks	*Cephus*	*Collyria*	Percentage parasitism	*Cephus*	*Collyria*	Percentage parasitism
1933 ...	242	50·9	25·0	49	50·9	25·0	49
1934 ...	189	17·0	7·0	41	27·4	11·2	41
	101	19·3	6·4	33			
	227	22·3	16·3	73			
	158	36·0	7·0	19			
	230	42·4	19·1	45			
1935 ...	263	12·5	×	×	34·2	11·6(?)	21(?)
	237	19·0	×	×			
	286	29·0	×	×			
	216	47·3	8·6	19			
	241	63·2	14·6	23			
1936 ...	255	22·2	11·3	51	38·5	11·6	30
	306	25·0	5·7	23			
	226	47·0	15·4	33			
	222	60·0	14·0	23			
1937 ...	107	6·3	3·7	58	14·5	7·0	48
	99	8·7	4·7	54			
	168	10·0	6·0	60			
	204	15·5	6·5	42			
	140	17·4	6·9	40			
	223	28·9	14·1	49			
1938 ...	246	11·0	4·0	36	17·5	7·4	42
	156	12·3	5·3	43			
	264	15·7	6·7	43			
	281	16·2	7·0	43			
	275	16·8	6·0	36			
	279	22·7	10·0	44			
	209	27·8	13·1	47			

COLLECTIONS RECEIVED.

The following collections were received by the Imperial Institute of Entomology between 1st July and 30th September, 1939 :—

Agricultural Research Institute, Wad Medani :—22 Diptera, 27 Parasitic Hymenoptera, 38 Lepidoptera, 22 species of Aphidae, 9 other Rhynchota, and 96 Orthoptera ; from the Sudan.

Agricultural Superintendent, Antigua :—50 Isoptera.

Agricultural Superintendent, St. Kitts :—150 Isoptera.

Mr. M. D. Austin :—12 Parasitic Hymenoptera ; from England.

Dr. H. Blunck :—19 Parasitic Hymenoptera ; from Germany.

Mr. H. E. Box :—700 Formicidae and 68 slide preparations of Lepidoptera ; from various localities.

Prof. P. A. Buxton, London School of Tropical Medicine :—35 Diptera ; from England.

Mr. E. McC. Callan :—300 Parasitic Hymenoptera ; from Trinidad.

Mr. F. C. Camargo :—1 Curculionid ; from Brazil.

Mr. J. Carroll :—6 Dipterous larvae ; from Ireland.

Mr. B. J. Catton :—18 Orthoptera ; from Turkey.

Dr. A. Chiaromonte :—7 Coleoptera, 99 Parasitic Hymenoptera, and 2 Lepidoptera ; from Abyssinia.

Chief Entomologist, Pretoria :—100 Diptera, 75 Coleoptera, 19 Parasitic Hymenoptera, 8 Lepidopterous pupa-cases, 9 Rhynchota, and 24 Orthoptera ; from South Africa.

Chief Plant Protection Officer, Jerusalem :—8 Coleoptera and 32 Parasitic Hymenoptera ; from Palestine.

Mr. L. D. Cleare, Government Entomologist :—45 Diptera and 9 puparia, 54 Coleoptera, 40 Parasitic Hymenoptera, 85 Isoptera, 2 species of Coccidae, 22 other Rhynchota, and 5 Mallophaga ; from British Guiana.

Colombo Museum :—88 Diptera ; from South India.

Colonial Secretary, Gambia :—70 Isoptera.

Conservator of Forests, British Honduras :—14,600 Isoptera.

Mr. G. H. Corbett, Government Entomologist :—113 Diptera, 56 Coleoptera, 64 Parasitic Hymenoptera, 36 Formicidae, 35 Lepidoptera, 700 Isoptera, 16 Rhynchota, 3 Orthoptera, and 2 Plecoptera ; from Malaya.

Coryndon Memorial Museum, Nairobi :—14 Lepidoptera ; from Kenya Colony.

Mr. G. S. Cotterell, Government Entomologist :—45 Parasitic Hymenoptera ; from the Gold Coast.

Mr. W. Cottier, Entomologist :—3 Curculionidae ; from New Zealand.

Mr. A. Cuthbertson, Entomologist :—76 Diptera, 15 Coleoptera, 2 Blattidae, and 2 Forficulidae ; from Southern Rhodesia.

Dr. A. Diakonoff :—30 Rhynchota ; from Java.

Director of Agriculture, Mauritius :—7 Diptera, 20 Coleoptera, and 200 Parasitic Hymenoptera.

Messrs. R. R. Douglas, Ltd :—Samples of Chillies attacked by Curculionidae ; from Nigeria.

Mr. S. Duvdevani :—3 Parasitic Hymenoptera ; from Palestine.

Mr. R. G. Fennah, Entomologist :—110 Coleoptera, 50 Parasitic Hymenoptera, 150 Isoptera, and 6 Rhynchota ; from the British West Indies.

Dr. K. R. Fischer :—3 Diptera and 2 pupa-cases, and 21 Parasitic Hymenoptera ; from Germany.

Mr. J. L. Froggatt, Government Entomologist :—2 Diptera, 20 Coleoptera, 126 Parasitic Hymenoptera, 300 other Hymenoptera, 12 Lepidoptera, 20 Isoptera, 2 species of Aphidae, 10 other Rhynchota, 2 Orthoptera, and 100 Ticks ; from New Guinea.

Game Warden, Nairobi :—100 Ephemerid early stages, 5 Trichopterous early stages, 30 Turbellaria, and 12 Snails ; from Kenya Colony.

Mr. J. C. M. Gardner, Systematic Entomologist :—121 Diptera, 17 Coleoptera and 2 larvae, 29 Parasitic Hymenoptera and 8 cocoons ; from the United Provinces, India.

Mr. P. F. Garthwaite, Forest Entomologist :—1 Ichneumonid ; from Burma.

Mr. F. D. Golding, Government Entomologist :—2 Diptera, 13 Coleoptera, 54 Lepidoptera, 9 Rhynchota, 12 Orthoptera, and 3 Hemimeridae ; from Nigeria.

Government Entomologist, Coimbatore :—4 Diptera and 4 pupa-cases, 43 Coleoptera, and 9 Lepidoptera ; from South India.

Government Entomologist, Lyallpur :—28 Dipterous larvae, 27 Coleoptera, 31 Parasitic Hymenoptera, 28 Lepidoptera and 6 larvae, 50 Isoptera, 1 species of Coccidae, 4 other Rhynchota, and 11 Orthoptera ; from the Punjab, India.

Government Secretary, Basutoland :—100 Isoptera.

Governor, Somaliland :—11 Coleoptera and 6 early stages, 119 Formicidae, 2 Hymenopterous larvae, and 230 Isoptera.

Dr. A. J. Hesse :—1 Curculionid ; from South Africa.

Prof. W. E. Hoffmann :—235 Orthoptera ; from China.

Dr. J. C. Hutson, Government Entomologist :—4 Parasitic Hymenoptera ; from Ceylon.

Imperial Entomologist, New Delhi :—23 Diptera, 54 Coleoptera, 31 Lepidoptera, and 19 Rhynchota ; from India.

Institute for Plant Diseases, Buitenzorg :—85 Coleoptera, 750 Parasitic Hymenoptera, 62 Lepidoptera, and 32 Rhynchota ; from the Dutch East Indies.

Miss D. J. Jackson :—16 Parasitic Hymenoptera ; from Scotland.

Mr. C. J. Joubert :—30 Curculionidae ; from South Africa.

Mr. C. B. R. King, Tea Research Entomologist :—4 Parasitic Hymenoptera ; from Ceylon.

Dr. W. A. Lamborn, Medical Entomologist :—400 Siphonaptera, 15 Ticks, and 80 Mites ; from Nyasaland.

Mr. O. B. Lean :—2 Coleoptera ; from England.

Mr. R. A. Lever, Government Entomologist :—36 Siphonaptera, 10 Culicidae, 186 other Diptera, and 4 pupa-cases, 205 Coleoptera and 6 early stages, 74 Parasitic Hymenoptera, 3 other Hymenoptera, 86 Lepidoptera, 11 Thysanoptera, 2 species of Aphidae, 51 other Rhynchota, 3 Orthoptera, 4 Dermaptera, 2 Odonata, and 11 Trichoptera ; from the Fiji Islands.

Mr. A. R. Melville, Entomologist :—50 Diptera and early stages ; from Uganda.

Dr. A. Meuche :—28 Parasitic Hymenoptera ; from Germany.

Dr. J. Mombaerts :—18 Parasitic Hymenoptera ; from Belgium.

Dr. O. Monte :—8 Curculionidae and 2 Rhynchota ; from Brazil.

Mr. N. S. Noble :—24 Parasitic Hymenoptera ; from New South Wales.

Mr. J. Risbec :—18 Diptera, 369 Coleoptera and 17 early stages, 409 Parasitic Hymenoptera, 8 other Hymenoptera, 22 Lepidoptera, and 5 pupae, 2 species of Coccidae, 47 other Rhynchota, 51 Orthoptera, and 22 Millipedes ; from Senegal.

Dr. H. Sachtleben :—1,200 Parasitic Hymenoptera ; from Germany.

Selangor Museum, Kuala Lumpur :—231 Coleoptera, 2 Parasitic Hymenoptera, and 2 Lepidoptera ; from Malaya.

Dr. A. Shulov :—25 Siphonaptera, 6 Diptera, 36 Coleoptera, 161 Parasitic Hymenoptera, 10 other Hymenoptera, 22 Lepidoptera, 50 Thysanoptera, 11 species of Coccidae, 13 species of Aphidae, 120 other Rhynchota, 5 Thysanura, and 6 Collembola ; from Palestine.

Mr. C. B. Symes, Medical Entomologist :—30 Psychodidae and 2 Ephemerid larvae ; from Kenya Colony.

Dr. R. Takahashi :—7 Parasitic Hymenoptera ; from Japan.

Mr. T. H. C. Taylor, Entomologist :—5 Diptera, 393 Coleoptera, 152 Rhynchota, and 9 Planipennia ; from Uganda.

Dr. O. Theodor :—355 Diptera, 34 Coleoptera, 4 Parasitic Hymenoptera, and 5 Embiidae ; from Palestine.

Mr. W. H. Thorpe :—50 Parasitic Hymenoptera ; from Tanganyika Territory.

Veterinary Research Officer, Entebbe :—1 *Glossina* ; from Uganda.

Mr. J. M. Waterston, Plant Pathologist :—52 Coleoptera and 3 early stages, 26 Formicidae, and 200 Isoptera ; from Bermuda.

Mr. F. Wilson :—2 Diptera, 6 Hymenoptera, and 7 Lepidoptera ; from France.

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